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Random dispersal versus fitness-dependent dispersal

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ABSTRACT

This work extends previous work (Cantrell et al., 2008 [9]) on fitness-dependent dispersal for a single species to a two-species competition model. Both species have the same population dynamics, but one species adopts a combination of random and fitness-dependent dispersal and the other adopts random dispersal. Global existence of smooth solutions to the time-dependent quasilinear parabolic system is studied. When a single species has a strong tendency to move up its fitness gradient, it results in a stable equilibrium that can approximate the spatial distribution predicted by the ideal free distribution (Cantrell et al., 2008 [9]). For the two-species competition model, if one species has strong tendency to move up its fitness gradient, such approximately ideal free dispersal is advantageous relative to random dispersal. Bifurcation analysis shows that two competing species can coexist when one species has only an intermediate tendency to move up its fitness gradient and the other species has a smaller random dispersal rate.

1. Introduction

This work extends our previous work [9] on fitness-dependent dispersal for a single species to a two-species competition model, with one species adopting a combination of random and fitness-dependent dispersal and the other adopting random dispersal. The model we considered in [9] has the form

$$\begin{cases} u_t = \nabla\cdot\big[\mu\nabla u - \alpha u\nabla f(x,u)\big] + uf(x,u) & \text{in } \Omega\times\mathbb{R}_+, \\ \big[\mu\nabla u - \alpha u\nabla f(x,u)\big]\cdot n = 0 & \text{on } \partial\Omega\times\mathbb{R}_+, \end{cases} \tag{1.1}$$

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where $\mathbb{R}_+ = (0, \infty)$, and

$$f(x,u) = m(x) - u. \tag{1.2}$$

The function $u(x,t)$ represents the density of a single species with random diffusion coefficient μ, and α measures the tendency of the species to move upward along the gradient of the fitness of the species, measured by $f(x,u)$. We assume that μ is a positive constant and α is a non-negative constant. Ω is a bounded region in $\mathbb{R}^N$ with boundary $\partial\Omega$, and n denotes the outward unit normal vector on $\partial\Omega$. Throughout this paper we assume that $m \in C^{2,\gamma}(\overline{\Omega})$ for some $\gamma \in (0,1)$ and m is positive somewhere in Ω, and $u(x,0)$ is continuous, non-negative and not identically zero in $\overline{\Omega}$. We briefly summarize some of the main results in [9] as follows:

- (Global existence in time) Suppose that $\mu > 0$ and $\alpha \geqslant 0$. Then (1.1) has a unique solution $u \in C^{2,1}(\overline{\Omega} \times (0,\infty)) \cap C(\overline{\Omega} \times [0,\infty))$.
- (Existence of positive steady state) If $u = 0$ is linearly unstable, then (1.1) has at least one positive steady state. Note that if $\int_\Omega m > 0$, $u = 0$ is linearly unstable for any $\mu > 0$ and $\alpha \geqslant 0$.
- (Global attractor) If $m > 0$ in $\overline{\Omega}$, then for large α/μ, (1.1) has a unique positive steady state which is also globally asymptotically stable.

To study the evolution of dispersal, a common approach, initiated by Hastings [24] for reaction–diffusion models, is to consider models of two populations that are ecologically identical but use different dispersal strategies. In general, using such a modeling approach would lead to a system of the form

$$\begin{cases} u_t = \nabla \cdot \big[\mu \nabla u - \alpha u \nabla f(x, u+v)\big] + u f(x, u+v) & \text{in } \Omega \times \mathbb{R}_+, \\ v_t = \nabla \cdot \big[\nu \nabla v - \beta v \nabla g(x,u,v)\big] + v f(x, u+v) & \text{in } \Omega \times \mathbb{R}_+, \\ \big[\mu \nabla u - \alpha u \nabla f(x,u+v)\big] \cdot n = \big[\nu \nabla u - \beta u \nabla g(x,u,v)\big] \cdot n = 0 & \text{on } \partial\Omega \times \mathbb{R}_+, \end{cases} \tag{1.3}$$

where f is as in (1.2), and g represents part of an alternate dispersal strategy. For example, $g = 0$ would correspond to unconditional dispersal of organisms by simple diffusion, $g = m$ would correspond to advection up resource gradient without consideration of crowding, while $g = -(u+v)$ would correspond to avoidance of crowding without reference to resource distribution. We refer to [3–5,7–11,13,14,17,23,27,30–32,42,38,46] for recent progress in this direction for reaction–diffusion models.

In this paper we will focus on system (1.3) with $g = 0$, i.e.,

$$\begin{cases} u_t = \nabla \cdot \big[\mu \nabla u - \alpha u \nabla f(x, u+v)\big] + u f(x, u+v) & \text{in } \Omega \times \mathbb{R}_+, \\ v_t = \nu \Delta v + v f(x, u+v) & \text{in } \Omega \times \mathbb{R}_+, \\ \big[\mu \nabla u - \alpha u \nabla f(x,u+v)\big] \cdot n = \nabla v \cdot n = 0 & \text{on } \partial\Omega \times \mathbb{R}_+, \end{cases} \tag{1.4}$$

where the initial conditions $u(x,0)$ and $v(x,0)$ are non-negative and not identically zero in $\overline{\Omega}$, and μ, ν, α are all positive constants.

Theorem 1. *Suppose that $\Omega \subset \mathbb{R}^N$ with $\partial\Omega$ of class $C^{2+\gamma}$, $m \in C^{2+\gamma}(\overline{\Omega})$ for some $\gamma \in (0,1)$. Then solutions of system (1.4) with bounded non-negative initial data exist globally for $N = 1, 2$, and also for $N \geqslant 3$ provided that $\nu > \mu$.*

It is an open question whether solutions of system (1.4) with bounded non-negative initial data exist globally for $N \geqslant 3$ and $\nu \leqslant \mu$.

For the rest of this section our discussion will mainly focus on non-negative and non-trivial steady states of system (1.4). System (1.4) has two semi-trivial steady states, denoted by $(\tilde{u}, 0)$ and $(0, \theta)$

respectively, where $\tilde{u}$ is a positive steady state of the scalar equation (1.1), and θ is a positive solution of the scalar equation

$$\nu\Delta\theta + \theta(m-\theta) = 0 \quad \text{in } \Omega, \qquad \nabla\theta\cdot n = 0 \quad \text{on } \partial\Omega. \tag{1.5}$$

For the existence of $\tilde{u}$, we need to assume that $u = 0$ is linearly unstable in (1.1). For that to be the case, a sufficient condition is that the principal eigenvalue, denoted by $\lambda^*(\mu,\alpha)$, of the associated eigenvalue problem

$$\nabla\cdot[\mu\nabla\phi - \alpha\phi\nabla m] + m\phi = -\lambda\phi \quad \text{in } \Omega, \qquad [\mu\nabla\phi - \alpha\phi\nabla m]\cdot n = 0 \quad \text{on } \partial\Omega \tag{1.6}$$

is strictly negative. Similarly, θ exists if and only if $\lambda^*(\nu,0) < 0$; moreover, θ is unique whenever it exists. In particular, if $\int_\Omega m > 0$, then $\tilde{u}$ exists for any $\alpha \geqslant 0$ and $\mu > 0$, and θ exists for any $\nu > 0$.

System (1.4) with $\alpha = 0$ has been studied in Dockery et al. [20] in the context of evolution of random dispersal in spatially homogeneous and temporally constant environments, and the general conclusion is that slower dispersal will evolve; see also [24,26,28]. In particular, it is shown in [20] that if $\alpha = 0$, m is non-constant and $\mu < \nu$, then $(\tilde{u}, 0)$ is globally asymptotically stable whenever $(\tilde{u}, 0)$ exists. When α is small positive, the following result can be established easily by using an approach similar to that in [20]:

Theorem 2. *Suppose that m is non-constant and positive somewhere in Ω.*

(i) *If $\mu < \nu$, then for small positive α, $(\tilde{u}, 0)$ is linearly stable and $(0, \theta)$ is linearly unstable, whenever they exist.*
(ii) *If $\mu > \nu$, then for small positive α, $(\tilde{u}, 0)$ is linearly unstable and $(0, \theta)$ is linearly stable, whenever they exist.*

Next we consider the case when α is sufficiently large. This case, if restricted to the single species equation (1.1), corresponds to the scenario when the species u, at equilibrium, reaches an approximately ideal free distribution. More precisely, if $\alpha \to \infty$, $\tilde{u} \to m_+$ uniformly in $\overline{\Omega}$, i.e., the population density approximately matches the availability of resources. Therefore, we predict that for large α, such approximately ideal free dispersal allows a population to better track the distribution of resources so that it is likely to be more advantageous than other sorts of dispersal strategies including random dispersal. Our next few results strongly support this prediction.

To understand the dynamics of system (1.4), it is important to study the stability of semi-trivial steady states $(\tilde{u}, 0)$ and $(0, \theta)$. Biologically, the stability of $(\tilde{u}, 0)$ is associated with the question of invasibility, namely, what happens when the species with density u is at equilibrium and a small number of a mutant species with density v is introduced. Can the species with density v invade when rare? Mathematically, the stability of $(\tilde{u}, 0)$ is determined by the smallest eigenvalue, denoted by $\lambda_u(\alpha,\mu,\nu)$, of the linear problem

$$\nu\Delta\psi + (m-\tilde{u})\psi = -\lambda\psi \quad \text{in } \Omega, \qquad \nabla\psi\cdot n|_{\partial\Omega} = 0.$$

More precisely, $(\tilde{u}, 0)$ is linearly stable if $\lambda_u > 0$ and linearly unstable if $\lambda_u < 0$. The following result addresses this issue when α is sufficiently large.

Theorem 3. *Suppose that either m changes sign in $\overline{\Omega}$, or $m > 0$ in $\overline{\Omega}$ and m is non-constant. Then for any ν and $\eta > 0$, there exists some positive constant $\Lambda_1 = \Lambda_1(\nu, \eta, m, \Omega)$ such that if $\alpha \geqslant \eta$ and $\alpha/\mu \geqslant \Lambda_1$, $(\tilde{u}, 0)$ is linearly stable.*

Theorem 3 ensures that if the species with density u is at equilibrium and is adopting an approximately ideal free dispersal strategy, the species with density v, which is adopting a random dispersal strategy, cannot invade when rare. This implies that random dispersal compares unfavorably to an approximately ideal free dispersal strategy. It is unknown whether the conclusions of Theorem 3 still hold in the case when m is non-negative and the set where m is equal to zero is non-empty.

An opposite question is: if the species with density v is at equilibrium, can the species with density u invade when rare? This question is related to the stability of $(0,\theta)$. Mathematically, the linear stability of $(0,\theta)$ is determined by the smallest eigenvalue, denoted by $\lambda_v(\alpha,\mu,\nu)$, of the linear problem

$$\begin{cases} \nabla\cdot\big[\mu\nabla\varphi-\alpha\varphi\nabla(m-\theta)\big]+\varphi[m-\theta]=-\lambda\varphi \quad \text{in } \Omega, \\ \big[\mu\nabla\varphi-\alpha\varphi\nabla(m-\theta)\big]\cdot n|_{\partial\Omega}=0. \end{cases} \tag{1.7}$$

More precisely, $(0,\theta)$ is linearly stable if $\lambda_v>0$ and linearly unstable if $\lambda_v<0$. The following result addresses the linear stability of $(0,\theta)$ for sufficiently large α.

Theorem 4. *Suppose that m is non-constant and positive somewhere in Ω. Then for any ν, there exists some positive constant $\Lambda_2=\Lambda_2(\nu,m,\Omega)$ such that if $\alpha/\mu\geqslant\Lambda_2$, $(0,\theta)$ is always unstable whenever it exists, where $\Lambda_2>0$ is uniquely determined by*

$$\int_\Omega (m-\theta)e^{\Lambda_2(m-\theta)}=0. \tag{1.8}$$

Theorem 4 implies that if the species with density v is at equilibrium and is adopting a random dispersal strategy, then species with density u, which is taking an approximately ideal free dispersal strategy, can always invade when rare. This again implies that random dispersal compares unfavorably to an approximately ideal free dispersal strategy. We conjecture that if α is sufficiently large, then the semi-trivial steady state $(\tilde{u},0)$ is the global attractor of (1.4) among non-negative, not identically zero initial data. This conjecture is further supported by the following result on positive steady states of (1.4) with large α:

Theorem 5. *Suppose that function $m(x)$ changes sign in Ω. Then for any μ, ν, there exists some positive constant $\Lambda_3=\Lambda_3(\mu,\nu,m,\Omega)$ such that if $\alpha\geqslant\Lambda_3$, system (1.4) has no positive steady states.*

It is an open question whether Theorem 5 still holds when m is non-negative in $\overline{\Omega}$.

Given any $\mu>\nu$, from Theorems 2, 3 and 4 we see that, under suitable assumptions on m, both $(\tilde{u},0)$ and $(0,\theta)$ will change stability at least once when α varies from zero to infinity. In the following we show that under certain conditions $(0,\theta)$ changes its stability exactly once as α varies from zero to large.

Theorem 6. *Suppose that Ω is convex and the Hessian matrix of m is negative definite for every $x\in\overline{\Omega}$. Then, there exists some $\nu_0=\nu_0(m,\Omega)>0$ such that*

(i) *if $\nu>\max\{\nu_0,\mu\}$, $(0,\theta)$ is linearly unstable for every $\alpha\geqslant 0$;*
(ii) *if $\mu>\nu>\nu_0$, there exists a unique $\alpha^*=\alpha^*(\mu,\nu,m,\Omega)>0$ such that $(0,\theta)$ is linearly stable for every $\alpha\in[0,\alpha^*)$ and linearly unstable for every $\alpha\in(\alpha^*,\infty)$.*

A natural question is whether this uniquely determined α^*, when it exists, is a bifurcation point. Our next result not only gives an affirmative answer to this question but also provides some information on the global bifurcation diagram of positive steady states.

Theorem 7. *Suppose that Ω is convex, the Hessian matrix of m is negative definite for every $x\in\overline{\Omega}$, and $\mu>\nu>\nu_0$.*

(1) *(Local bifurcation) There exist some* $\epsilon > 0$ *and continuous functions* $\alpha : (\alpha^* - \epsilon, \alpha^* + \epsilon) \to \mathbb{R}$ *and* $\varphi(s), \psi(s) : (-\epsilon, \epsilon) \to C^2(\overline{\Omega})$ *such that* $\alpha(0) = \alpha^*$, $\varphi(0) = \varphi^*$ *for some positive function* φ^*, $\psi(0) = \psi^*$, *and solutions of system* (1.4) *near* $(\alpha^*, 0, \theta)$ *consist precisely of* $(\alpha, 0, \theta)$ *and* $\{(\alpha(s), s\varphi(s), \theta + s\psi(s))\}$, $s \in (-\epsilon, \epsilon)$.

(2) *(Global bifurcation) Further assume that* $m(x)$ *changes sign in* Ω. *Then the componentwise positive equilibria to* (1.4) *which emanate from* $(\alpha, 0, \theta)$ *at* $(\alpha^*, 0, \theta)$ *contain a continuum which meets* $(\alpha^{**}, \tilde{u}, 0)$, *where* $\tilde{u}$ *is a positive equilibrium solution of* (1.1) *for* $\alpha = \alpha^{**}$.

Since $\varphi^* > 0$ in $\overline{\Omega}$, $(s\varphi(s), \theta + s\psi(s))$ is a positive steady state of (1.4) with $\alpha = \alpha(s)$ for every $0 < s < \epsilon$. In other words, part (i) of Theorem 7 ensures that a branch of positive steady states of (1.4) bifurcates from $(0, \theta)$ at $\alpha = \alpha^*$. Moreover, under the assumptions of Theorem 7, by Theorem 6, α^* is the only bifurcation point for $(0, \theta)$. Part (ii) implies that the branch of positive steady states of (1.4) which bifurcates from $(\alpha, 0, \theta)$ at $(\alpha^*, 0, \theta)$ contains a continuum which meets the other semi-trivial steady state $(\alpha^{**}, \tilde{u}, 0)$. For our bifurcation analysis we use the framework given by Shi and Wang in [44], which builds on work by various authors including Dancer, Fitzpatrick, López-Gómez, Pejsachowicz, and Rabier; see [44] for details and references.

For general m, it is an open question whether there is a unique bifurcation point for $(\tilde{u}, 0)$ or $(0, \theta)$. To further illuminate this issue, we turn to discuss the asymptotic behaviors of all possible bifurcation points as $\mu \to \infty$ or $\nu \to 0$. Numerical simulations suggest that, as α varies from zero to infinity, the two competing species coexist for some intermediate interval of α. More precisely, if α is the bifurcation parameter, a branch of positive steady states bifurcates from $(\tilde{u}, 0)$ at some $\alpha = \alpha_u$ and it connects to $(0, \theta)$ at some $\alpha = \alpha_v$. How do these two bifurcation values α_u and α_v depend upon values of μ and ν? To address this question, we first give precise definitions of the values α_u and α_v. For any $\mu > \nu > 0$, both $\lambda_u(\alpha, \mu, \nu) = 0$ and $\lambda_v(\alpha, \mu, \nu) = 0$ have at least one positive root. Let $\alpha_u(\mu, \nu)$ denote any positive root of $\lambda_u(\alpha, \mu, \nu) = 0$ and let $\alpha_v(\mu, \nu)$ denote any positive root of $\lambda_v(\alpha, \mu, \nu) = 0$. Simulation results suggest that for each fixed $\nu > 0$, as μ becomes large, the coexistence interval becomes wider and both ends of the coexistence interval approach infinity as $\mu \to \infty$. This suggests that as $\mu \to \infty$, both α_u and α_v tend to infinity. In the following we give some characterizations of asymptotic behaviors of α_u and α_v as $\mu \to \infty$.

Theorem 8. *Fix* $\nu > 0$. *Then,*

(a) *subject to passing to a subsequence,* $\lim_{\mu\to\infty} \alpha_u(\mu, \nu)/\mu = \Lambda^*$, *where* $\Lambda^* > 0$ *is chosen such that the following system has a positive solution* (u^*, φ^*):

$$\begin{cases} \Lambda^*\big(m - u^*\big) = \ln u^* - \dfrac{\int_\Omega u^* \ln u^*}{\int_\Omega u^*} \quad \text{in } \Omega, \\ \nu\Delta\varphi^* + \big(m - u^*\big)\varphi^* = 0 \quad \text{in } \Omega, \quad \nabla\varphi^* \cdot n|_{\partial\Omega} = 0. \end{cases} \tag{1.9}$$

(b) $\lim_{\mu\to\infty} \alpha_v(\mu, \nu)/\mu = \Lambda_2$, *where* $\Lambda_2 > 0$ *is uniquely determined by* (1.8).

Remark 1.1. We know that Λ^* exists and is positive, but we do not know yet whether such Λ^* is unique. This probably explains why it is in general difficult to show that there is at most one bifurcation point for $(\tilde{u}, 0)$.

Simulation results also suggest that for each fixed $\mu > 0$, as ν becomes sufficiently small, the coexistence interval also becomes wider and both ends of the coexistence interval approach infinity as $\nu \to 0$. This suggests that as $\nu \to 0$, both α_u and α_v tend to infinity. In the following result we give some characterization of asymptotic behaviors of α_u as $\nu \to 0$.

Theorem 9. *Fix* $\mu > 0$. *Then*

$$\lim_{\nu\to 0} \frac{\alpha_u(\mu, \nu)}{\mu/\nu} = \Lambda^{**},$$

where $\Lambda^{**} > 0$ *is the unique positive number such that the following equation has a positive solution*:

$$-\Lambda^{**}\Delta\varphi + \left[\frac{\int_\Omega m \ln m}{\int_\Omega m} - \ln m\right]\varphi = 0 \quad \text{in } \Omega, \qquad \nabla\varphi \cdot n|_{\partial\Omega} = 0.$$

We are unable to determine the asymptotic behavior of α_ν as $\nu \to 0$.

This paper is organized as follows. In Section 2 we study the global existence of solutions of (1.4) and establish Theorem 1. The linear stability of both semi-trivial steady states is considered in Sections 3, 4 and 6, and we prove Theorems 3, 4 and 6, respectively. Section 5 is devoted to the proof of Theorem 5, the non-existence of positive steady states of (1.4). In Section 6 we study the local and global bifurcation diagram of positive steady states of (1.4) and prove Theorem 7. Asymptotic behaviors of bifurcation points are investigated in Section 7, and we prove Theorems 8 and 9 there. Finally in Section 8, numerical simulation results on various consumer–resource models are presented to suggest future directions.

2. Preliminary results and global existence

We will always assume that Ω is a bounded domain in $\mathbb{R}^N$ for some N. The local existence of solutions follows from the results of [1]. Showing the global existence of solutions requires some additional analysis. The system (1.4) is triangular and, in the terminology of [2], it is affine in the gradient. Thus, Theorem 3 of [2] applies, so that for global existence it is sufficient to establish that solutions on any finite interval $(0, T]$ are bounded in L^∞, where the bound may depend on T and the initial data. In fact, an extension of the results of [2] derived in [34] that requires an L^∞ bound on v but only an L^p bound on u with p sufficiently large can be applied to (1.4). The system (1.4) is similar in structure to cross-diffusion models, and it turns out that it can be treated by some of the methods developed for those models, as we will describe later in this section. First we note that since (1.4) is a model for population densities we are interested only in non-negative solutions.

Proposition 1. *If u and v satisfy the equations and boundary conditions of* (1.4) *for $t \in (0, T]$ with $u(x,0), v(x,0) \geqslant 0$ then $u, v \geqslant 0$ for $t \in [0, T]$.*

Proof. From the form of the equation and boundary condition for v it is clear by the maximum principle [43] that if $v(x,0) \geqslant 0$ then $v \geqslant 0$ on $\Omega \times [0, T]$. Let $z = ue^{(\alpha/\mu)(u-m)}$. In view of the boundary condition on v, the boundary condition on u is equivalent to $(\mu + \alpha u)\partial u/\partial n - \alpha u \partial m/\partial n = 0$ on $\partial\Omega \times (0, T]$. Using this fact we can see that z satisfies

$$\begin{cases} z_t = \big[1 + (\alpha/\mu)u\big]\big\{\mu\Delta z + \alpha[\nabla m - \nabla u + \nabla v]\cdot\nabla z \\ \qquad + \big[(\alpha^2/\mu)(\nabla m - \nabla u)\cdot\nabla v + \alpha\Delta v + f(x,u,v)\big]z\big\} \quad \text{in } \Omega \times (0, T], \\ \dfrac{\partial z}{\partial n} = 0 \quad \text{on } \partial\Omega \times (0, T]. \end{cases} \tag{2.1}$$

Since $u(x,0) \geqslant 0$ it follows that $\mu + \alpha u > 0$ for $t \in [0, \delta]$ for some $\delta > 0$. By the form of (2.1) it follows from the maximum principle that $z \geqslant 0$ on $[0, \delta]$, so $u \geqslant 0$ on $[0, \delta]$. Let $t_0 > 0$ be the largest value of $t \in [0, T]$ such that $u \geqslant 0$ for $t \leqslant t_0$. If $t_0 < T$ then since $u(x, t_0) \geqslant 0$ we can argue as before that z and hence u must be non-negative for $t \in [0, t_0 + \delta]$ for some $\delta > 0$, contradicting the definition of t_0. Thus, we must have $u \geqslant 0$ for $t \in [0, T]$. □

2.1. Normal ellipticity in existence and bifurcation theory

Before turning to the detailed analysis of the system (1.4) we will show that the differential operator on the right-hand side has a key property called *normal ellipticity*. It turns out that normal ellipticity is in some sense an optimal condition for local existence results based on semigroup theory (see [1, p. 16]) and is also important as a general condition implying that certain operators occurring in the bifurcation analysis of quasilinear systems are Fredholm with index zero (see [44, Section 2, especially Theorem 2.7 and its corollaries]). Suppose that an $n \times n$ system of linear second order differential operators on a domain $\Omega \subset \mathbb{R}^N$ has principal symbol $A(x,\xi) = \sum_{i,j=1}^N a_{ij}(x)\xi_i\xi_j$ where $a_{ij} = (a_{ij}^{rs})$ is an $n \times n$ matrix for $i, j = 1 \dots N$. The system is normally elliptic if the spectrum of the matrix $A(x,\xi)$ is contained in $\{z \in \mathbb{C}\colon\ \mathit{Re}\, z > 0\}$ for all $x \in \overline{\Omega}$ and $\xi \in \mathbb{R}^N \setminus \{0\}$. (See [1,2,44]. The way that the condition is formulated in [44] is slightly different from the formulation of [1,2] but the formulations are equivalent.) Detailed discussions of conditions for systems to be normal elliptic, the relation of normal ellipticity to uniform ellipticity and other ellipticity conditions, and the regularity results that follow from normal ellipticity are given in [1,44]. In particular, uniform ellipticity typically requires that $A(x,\xi)$ is positive definite in some sense, while normal ellipticity does not, so that appropriate forms of uniform ellipticity imply normal ellipticity, but normal ellipticity does not imply uniform ellipticity. It is noted on p. 2790 of [44] that the full proofs of certain L^p estimates stated in [1] are not given in that paper, but the details are provided in [44], so the full details of Amann's approach are available in the literature. We will verify that in the system defined by (1.4) the system of differential operators on the right-hand side is normally elliptic if the coefficients are evaluated for $u = u(x)$, $v = v(x)$ with $u(x)$ and $v(x)$ non-negative. Before doing that we will briefly review some background on ellipticity and existence theory for quasilinear parabolic systems. The first observation is that the idea of normal ellipticity is important in developing existence theory for quasilinear systems of cross-diffusion type, including specifically (1.4). As noted previously, uniform ellipticity is a more classical but stronger concept of ellipticity than normal ellipticity. Classical approaches to existence theory use test functions or other methods to obtain what amount to energy estimates which in turn lead to inequalities that can be used to obtain the estimates needed for existence results; see for example [21] or [16] among many others. Those methods typically require some form of uniform ellipticity and do not necessarily apply to normally elliptic systems (see the comment at the bottom of p. 19 of [1]). The methods used by Amann in [1,2] are based on properties of analytic semigroups and the theory of interpolation spaces, and for that approach normal ellipticity is sufficient. That turns out to be important for the study of systems such as (1.4). In [1, Eqs. (7) and (8)], Amann gives an example of a cross-diffusion system similar to (1.4) and comments on p. 16 "if we were forced to impose the uniform strong ellipticity condition in our example (7),(8) it would not be possible to study solutions with non-negative initial values ($u_0 \geqslant 0$, $v_0 \geqslant 0$) in general." It is clear from the work of Amann [1] and the verification of the L^p estimates in [44] that normal ellipticity is the appropriate condition for local existence results. There is an important special case in which the estimates needed for global existence are somewhat easier, and where the condition for normal ellipticity becomes simpler. That is the case where the principal part of the elliptic operator, and hence the principal symbol, are upper triangular. In that case it is possible, roughly speaking, to start with estimates for the last equation of the system, which is coupled to the rest of the system only in lower order terms, use those to obtain estimates for the next to last equation, and then continue work upward through the system to obtain the necessary estimates. In the case of an upper triangular system the condition for normal ellipticity requires only that the diagonal terms in the principal symbol satisfy $\sum_{i,j=1}^N a_{ij}^{rr}(x)\xi_i\xi_j > 0$ for all $x \in \overline{\Omega}$ and $\xi \in \mathbb{R}^N \setminus \{0\}$, for $r = 1 \dots n$. (See [2, Eq. (0.2) on p. 220].) Our operator has principal part

$$\begin{pmatrix} \mu + \alpha u & \alpha u \\ 0 & \nu \end{pmatrix} \begin{pmatrix} \triangle u \\ \triangle v \end{pmatrix}. \tag{2.2}$$

The boundary condition has principal part

$$\begin{pmatrix} \mu + \alpha u & \alpha u \\ 0 & \nu \end{pmatrix} \begin{pmatrix} \nabla u \cdot n \\ \nabla v \cdot n \end{pmatrix}. \tag{2.3}$$

It follows that the principal symbol has the form

$$\begin{pmatrix} (\mu+\alpha u)|\xi|^2 & \alpha u|\xi|^2 \\ 0 & \nu|\xi|^2 \end{pmatrix}. \tag{2.4}$$

As long as u and v are non-negative the operator and boundary conditions satisfy the conditions given by Amann [1,2] for normal ellipticity. These conditions are explicated in case 3 of Remark 2.5 of [44], where in the notation of [44], the principal part of our system would be defined by taking

$$a(x) = \begin{pmatrix} \mu+\alpha u & \alpha u \\ 0 & \nu \end{pmatrix} \tag{2.5}$$

and $\alpha_{ij} = \delta_{ij}$ where δ_{ij} is the Kronecker delta. Normal ellipticity follows if

$$det \begin{pmatrix} \mu+\alpha u+\sigma & \alpha u \\ 0 & \nu+\sigma \end{pmatrix} \neq 0 \tag{2.6}$$

when $\sigma = 0$ or $arg\,\sigma \in [-\pi/2, \pi/2]$. The determinant is

$$(\mu+\alpha u+\sigma)(\nu+\sigma),$$

so since $\mu + \alpha u > 0$ for non-negative u, relation (2.6) is satisfied and hence our system is normally elliptic. We will need to verify that certain linearized operators associated with our system are also normally elliptic to establish the Fredholm properties needed to apply the bifurcation results from [44]. We will do that in Section 6. The analysis is similar to what is shown here.

2.2. Global existence

We now turn to the issue of showing global existence in (1.4). To obtain global existence requires additional estimates, including estimates that imply uniform Hölder continuity of solutions with respect to the time variable, which are difficult to obtain in general; see [2, p. 223]. However, our system (1.4) has the special feature of being upper triangular. It is noted in [2] that for such systems it suffices to obtain L^∞ bounds that are uniform in time; see Theorem 3 of [2]. This result of [2] has been improved by Dung Le in [34] for the case of 2×2 systems with the triangular form

$$\begin{cases} u_t = \nabla \cdot \big[P(u,v)\nabla u + R(u,v)\nabla v\big] + F(u,v) & \text{in } \Omega \times (0,\infty), \\ v_t = \nabla \cdot \big[Q(u,v)\nabla v\big] + G(u,v) & \text{in } \Omega \times (0,\infty), \\ P(u,v)\dfrac{\partial u}{\partial n} + R(u,v)\dfrac{\partial v}{\partial n} = \dfrac{\partial v}{\partial n} = 0 & \text{on } \partial\Omega \times (0,\infty). \end{cases} \tag{2.7}$$

The main result of [34, Theorem 2.2] shows that under suitable hypotheses on P, Q, R, F and G (given in Eqs. (2.2)–(2.6) of [34]), it suffices to obtain a uniform L^∞ bound on v and a uniform L^N bound on u. It is simple to obtain L^∞ bounds on v in triangular systems like (1.4) and (2.7) because the form of equation and boundary condition for v allow the direct application of maximum principles or, more generally, invariance principles. The key issue is to obtain estimates for u. In general that is difficult to do, and in fact global existence is still an open question if $N \geqslant 3$ and $\nu \leqslant \mu$. In some cases global existence can be shown via methods developed by Dung Le and his collaborators. Those results, and some of the results of [2], again exploit the triangular structure of the system. Thus, they do not require uniform ellipticity conditions like those needed for general strongly coupled systems, for example as in [16]. We will discuss this point further in the remark and discussion following the next proposition.

Proposition 2. *(See [34, Theorem 2.2].) Suppose that $m \in C^{2+\gamma}(\overline{\Omega})$ and if $N > 1$ suppose that $\partial\Omega$ is of class $C^{2+\gamma}$ for some $\gamma \in (0,1)$. Suppose that (u,v) is a non-negative solution of (1.4) for $t \in I$, where I is an interval of existence of the solution. If $\|u\|_N$ and $\|v\|_\infty$ are uniformly bounded for $t \in I$ then so are $\|u\|_{C^{1+\delta}}$ and $\|v\|_{C^{1+\delta}}$ for some $\delta \in (0,1)$.*

Remark 2.1. Uniform bounds for u and v in $C^{1+\delta}$ for $t \in I$ imply that the solution (u,v) can be extended to some larger interval. If for any finite interval of existence I there is some uniform bound for u and v in $C^{1+\delta}$, possibly depending on I, then the solution can always be extended, so if I is the maximal interval of existence for the solution (u,v) then $I = (0,\infty)$, that is, the solution exists globally. See [2,34]. If there is such a uniform bound that is independent of I and the initial conditions then solutions are in Le's terminology ultimately uniformly bounded, which is effectively a type of dissipativity condition that implies the system has a global attractor with finite Hausdorff dimension; see [34]. The case $N = 1$ was also treated in [33] for a related system. See also [45] for similar results in one dimension.

Discussion. The only ways that the form of (1.4) differs from that of (2.7) are the dependence of $f(x,u,v)$ on x via $m(x)$ and the presence of the advection term $-\alpha\nabla \cdot (u\nabla m)$ in (1.4), also arising from the dependence of m on x. The results of [34] do not require the system to be uniformly elliptic; they require only that hypotheses (H.1) and (H.2) (Eqs. (2.2)–(2.6)) are satisfied. The conditions that are imposed on P, Q and R in hypothesis (H.1) of [34] are that they are differentiable, their derivatives can be bounded by some powers of u and v, and that $P(u,v) \geqslant d > 0$, $Q(u,v) \geqslant d > 0$, and $|R(u,v)| < \Phi(v)u$ where $\Phi(v)$ is a continuous function. The reaction terms in (1.4) are the same as those considered in the example in Theorem 3.1 of [34] except for the fact that m depends on x. In fact, Theorem 3.1 of [34] would apply directly to our system in the case of $N = 2$ if our system did not have the x-dependent terms arising from $m(x)$ because the hypotheses (H.1) and (H.2) would be satisfied, and that is all that is required. It is worth noting that the systems studied by Le and Nguyen in [35] are not necessarily uniformly elliptic because the coefficient b_{11} in Eq. (1.4) of [35] can be arbitrarily large. We do not use the results of [35] directly, but they illustrate that uniform ellipticity or positive definiteness are not needed for applications of the general results of [34]. By carefully going through the calculations used to derive Theorem 3.1 of [34] one can verify that the proof of that result extends to our system, thus yielding global existence when $N = 2$. The method used in [34] uses an induction argument to show that u is uniformly bounded in $L^p(\Omega)$ for any p, then uses the bounds to obtain estimates on the undifferentiated terms in the equations that allow the application of parabolic regularity theory. The inductive step in bounding u is based on multiplying the equation for u by u^{2p-1} so as to obtain a bound for $\|u\|_{2p}$ from a bound for $\|u\|_p$. The terms corresponding to P, Q, and R in (1.4) are $\mu + \alpha u$, v, and αu, respectively. Those satisfy the hypothesis (H.1) of [34] that is needed for the calculations in the inductive step. The dependence of $uf(x,u,v)$ and $vf(x,u,v)$ on u and v is the same as some of forms assumed for F and G in [34]. The fact that $f(x,u,v)$ depends on x does not affect the calculations. In our case the advection term $-\alpha\nabla \cdot (u\nabla m)$ produces an extra term $\int_\Omega \alpha u\nabla m \cdot \nabla(u^{2p-1})\,dx$ on the right side of formula (2.21) of [34]. That term can be estimated by $C\int_\Omega |\nabla m||U\nabla U|\,dx$, where $U = u^p$. Since ∇m is bounded an estimate analogous to (2.24) of [34] can then be used to obtain the bound needed to continue the inductive step. The smoothness conditions on m and $\partial\Omega$ are used so that regularity theory can be applied as in the discussion following (2.32) of [34]. A result similar to Theorem 2.2 of [34] is also proved in [33] for a related system with $\Omega \subset \mathbb{R}^1$. That system has a slightly different form than (1.4) or (2.7) but the key estimates are all essentially the same and extend directly to (1.4), thus yielding global existence when $N = 1$.

Proposition 3. *Suppose that $\Omega \subset \mathbb{R}^1$ or $\Omega \subset \mathbb{R}^2$ with $\partial\Omega$ of class $C^{2+\lambda}$, and that $m \in C^{2+\lambda}(\overline{\Omega})$ for some $\lambda \in (0,1)$. Then solutions of the system in (1.4) with non-negative initial data exist globally, and in fact they are ultimately uniformly bounded in $[C^{1+\delta}]^2$ so that the system (1.4) has a global attractor with finite Hausdorff dimension.*

Proof. The bound on $\|u\|_1$ obtained in Lemma 3.3 of [34] is valid in any dimension. The remaining estimates needed for global existence for the case $N = 1$ are obtained in [33]. As noted previously, the system studied in [33] is slightly different from (1.4) but all the key estimates [33] are essentially the same as those needed to treat (1.4) and extend to that system. (The analysis in [34] is very similar to that in [33].) For the case of $\Omega \subset \mathbb{R}^2$, the estimates used in Section 3 of [34] to obtain a bound on $\|u\|_2$ carry over to (1.4) essentially without modification. Global existence then follows from Proposition 2 and the results and methods of [2] as in [34]. Furthermore, the bound obtained in Section 3 of [34] and the analogous bound in the one-dimensional case that follows from the analysis in [33] imply ultimate uniform boundedness, which as noted in the remark following Proposition 2 implies the existence of a global attractor. □

For $\Omega \subset \mathbb{R}^N$ with $N > 2$ we do not have a general proof for global existence. However, global existence can be shown for $\nu > \mu$ by adapting some ideas from [35]. The results of [35] do not seem to extend directly to (1.4) because of the terms involving advection along ∇m but part of the proof can be modified to obtain estimates on $\|u\|_p$ for any p.

Proposition 4. *Suppose that $\Omega \subset \mathbb{R}^N$ with $\partial\Omega$ of class $C^{2+\lambda}$, $m \in C^{2+\lambda}(\overline{\Omega})$ for some $\lambda \in (0,1)$, and $\nu > \mu$ in (1.4). Then solutions of the system in (1.4) with bounded non-negative initial data exist globally.*

Proof. We first observe that by the form of the second equation in (1.4), the maximum principle (and more general invariance principles) imply $\|v\|_\infty < C$ on the interval of existence for some constant C depending only on m and the initial data. Thus, we need only bound the L^N norm of u. If $H(u,v)$ is a smooth function then we can use (1.4) to compute

$$\begin{aligned}
\frac{1}{2}\frac{d}{dt}\int_\Omega H(u,v)^2\,dx &= \int_\Omega (HH_u u_t + HH_v v_t)\,dx \\
&= -\int_\Omega \nabla H \cdot \bigl\{H_u\bigl[(\mu+\alpha u)\nabla u + \alpha u\nabla v - \alpha u\nabla m\bigr] + H_v[\nu\nabla v]\bigr\}\,dx \\
&\quad - \int_\Omega H\bigl\{\nabla H_u \cdot \bigl[(\mu+\alpha u)\nabla u + \alpha u\nabla v - \alpha u\nabla m\bigr] + \nabla H_v \cdot [\nu\nabla v]\bigr\}\,dx \\
&\quad + \int_\Omega H[H_u u + H_v v] f\,dx.
\end{aligned} \tag{2.8}$$

Le and Nguyen [35] treated systems of the form (2.7) and observed that an optimal estimate for the integral corresponding to the one on the second line of (2.8) can be obtained by choosing H to satisfy

$$RH_u = (P - Q)H_v; \tag{2.9}$$

see Eqs. (3.3) and (3.4) of [35] and the related discussion. In our case solving (2.9) with $P = \mu + \alpha u$, $Q = \nu$, and $R = \alpha u$ leads to $H(u,v) = h(u + v + \gamma \ln u)$ where $\gamma = (\mu - \nu)/\alpha$ and h is any smooth function. For the present purpose it is convenient to take $h(z) = exp(kz)$ where $k > 0$ is a constant to be chosen later, so that

$$H(u,v) = exp\bigl(k[u + v + \gamma \ln u]\bigr), \tag{2.10}$$

and hence

$$\nabla H(u,v) = kH\biggl[\biggl(1 + \frac{\gamma}{u}\biggr)\nabla u + \nabla v\biggr]. \tag{2.11}$$

With this choice of H we have

$$\int_\Omega \nabla H \cdot \{H_u[(\mu+\alpha u)\nabla u + \alpha u \nabla v - \alpha u \nabla m] + H_v[\nu \nabla v]\}\,dx$$
$$= \int_\Omega (\mu+\alpha u)|\nabla H|^2 - k(\mu - \nu + \alpha u) H \nabla m \cdot \nabla H\,dx, \tag{2.12}$$

where we have used $(1+\frac{\gamma}{u})\alpha u = (\mu - \nu + \alpha u)$. Note that

$$\nabla H_u = k\left(1+\frac{\gamma}{u}\right)\nabla H - \left(\frac{k\gamma}{u^2}\right) H \nabla u \quad \text{and} \quad \nabla H_v = k \nabla H. \tag{2.13}$$

Thus

$$\int_\Omega H\{\nabla H_u \cdot [(\mu+\alpha u)\nabla u + \alpha u \nabla v] + \nabla H_v \cdot [\nu \nabla v]\}\,dx$$
$$= \int_\Omega k(\mu+\alpha u) H \nabla H \cdot \left[\left(1+\frac{\gamma}{u}\right)\nabla u + \nabla v\right] dx$$
$$- \int_\Omega \frac{k\gamma}{u^2} H^2 [(\mu+\alpha u)|\nabla u|^2 + \alpha u \nabla u \cdot \nabla v]\,dx. \tag{2.14}$$

Since $\mu + \alpha u = \nu + (1+\frac{\gamma}{u})\alpha u$ we have

$$(\mu+\alpha u)|\nabla u|^2 + \alpha u \nabla u \cdot \nabla v = \nu |\nabla u|^2 + \alpha u \nabla u \cdot \left[\left(1+\frac{\gamma}{u}\right)\nabla u + \nabla v\right]$$
$$= \nu|\nabla u|^2 + \alpha u \nabla u \cdot \frac{\nabla H}{kH}. \tag{2.15}$$

It follows that for k sufficiently large

$$\int_\Omega H\{\nabla H_u \cdot [(\mu+\alpha u)\nabla u + \alpha u \nabla v] + \nabla H_v \cdot [\nu \nabla v]\}\,dx$$
$$= \int_\Omega (\mu+\alpha u)|\nabla H|^2\,dx - \int_\Omega \frac{k\gamma\nu}{u^2} H^2 |\nabla u|^2\,dx - \int_\Omega \frac{\alpha\gamma}{u} H \nabla u \cdot \nabla H\,dx$$
$$\geqslant \frac{1}{2}\left(\int_\Omega (\mu+\alpha u)|\nabla H|^2\,dx - \int_\Omega \frac{k\gamma\nu}{u^2} H^2 |\nabla u|^2\,dx\right). \tag{2.16}$$

Fixing a sufficiently large value of k we can use (2.12) and (2.16) in (2.8) to obtain

$$\frac{1}{2}\frac{d}{dt}\int_\Omega H(u,v)^2\,dx \leqslant -\frac{3}{2}\int_\Omega (\mu+\alpha u)|\nabla H|^2\,dx + \frac{1}{2}\int_\Omega \frac{k\gamma\nu}{u^2} H^2 |\nabla u|^2\,dx$$

$$+\int_\Omega k(\mu-\nu+\alpha u)H\nabla m\cdot\nabla H\,dx+\int_\Omega \alpha uH\nabla H_u\cdot\nabla m\,dx$$
$$+\int_\Omega H[H_u u+H_v v]f\,dx. \tag{2.17}$$

The hypothesis $\nu>\mu$ implies that $\gamma<0$. The first integral on the second line of (2.17) can be estimated as

$$\int_\Omega k(\mu-\nu+\alpha u)H\nabla m\cdot\nabla H\,dx\leqslant\int_\Omega(\mu+\alpha u)\bigl(\epsilon|\nabla H|^2+C_\epsilon H^2\bigr)\,dx$$
$$\leqslant\epsilon\int_\Omega(\mu+\alpha u)|\nabla H|^2\,dx+\int_\Omega\bigl(C_{\epsilon,\delta}+\delta u^2\bigr)H^2\,dx \tag{2.18}$$

where $C_{\epsilon,\delta}$ depends on α, μ, ν, m and k. Using (2.13) the second integral on the second line of (2.17) can be written as

$$\int_\Omega \alpha uH\nabla H_u\cdot\nabla m\,dx=\int_\Omega \alpha uHk\left(1+\frac{\gamma}{u}\right)\nabla H\cdot\nabla m\,dx-\int_\Omega\left(\frac{k\alpha\gamma}{u}\right)H\nabla u\cdot\nabla m\,dx. \tag{2.19}$$

The first integral on the right side of (2.19) is identical to the integral on the left in (2.18) and can be estimated in the same way. The second integral on the right side of (2.19) can be estimated as

$$-\int_\Omega\left(\frac{k\alpha\gamma}{u}\right)H\nabla u\cdot\nabla m\,dx\leqslant C_\epsilon+\epsilon\int_\Omega\frac{H^2|\nabla u|^2}{u^2}\,dx. \tag{2.20}$$

Finally, in the last integral on the right in (2.17) we have

$$H[H_u u+H_v v]f=kH^2[\gamma+u+v][m-u-v]$$
$$\leqslant kH^2\left[C-\frac{1}{2}(u+v)^2\right]\leqslant CH^2-\frac{k}{2}u^2H^2. \tag{2.21}$$

By using the hypothesis that $\gamma=(\mu-\nu)/\alpha<0$ and the estimates in (2.18), (2.20), and (2.21) with ϵ and δ taken to be sufficiently small, we can conclude from (2.17) that for some constants C_1, C_2,

$$\frac{1}{2}\frac{d}{dt}\int_\Omega H^2\,dx\leqslant-\int_\Omega(\mu+\alpha u)|\nabla H|^2\,dx+C_1+C_2\int_\Omega H^2\,dx$$
$$\leqslant C_1+C_2\int_\Omega H^2\,dx, \tag{2.22}$$

where the constants C_1 and C_2 depend on the initial data, m, and the parameters in the system (1.4). We can conclude that on any finite interval $0\leqslant t\leqslant T$, we have $\int H^2\,dx\leqslant C$ for some C depending on the initial data, T, C_1, and C_2. Since $\|v\|_\infty$ is bounded and $H(u,v)$ grows exponentially in u as $u\to\infty$, it follows that $\|u\|_p$ is bounded on $[0,T]$ for any p. Taking $p=N$, we have global existence of solutions to (1.4) by Proposition 2. $\square$

Remark 2.2. It may be possible to apply other methods of obtaining global existence for cross-diffusion systems, for example those developed in [15,40,47], to the system (1.4), but the structure of the nonlinear diffusion terms in the systems considered in those works is different than in (1.4). It is worth noting that the system treated in [47] includes advection along a fitness gradient as well as cross diffusion. It may also be possible to adapt methods developed to treat chemotaxis models as in [45]. These are topics of interest for future research.

3. Stability of $(\tilde{u}, 0)$ for large α/μ

This section is devoted to the proof of Theorem 3.

Recall that $\tilde{u}$ is a positive solution of

$$\begin{cases} \nabla \cdot \big[\mu \nabla \tilde{u} - \alpha \tilde{u} \nabla (m - \tilde{u})\big] + \tilde{u}[m - \tilde{u}] = 0 & \text{in } \Omega, \\ \big[\mu \nabla \tilde{u} - \alpha \tilde{u} \nabla (m - \tilde{u})\big] \cdot n|_{\partial\Omega} = 0. \end{cases} \tag{3.1}$$

The stability of $(\tilde{u}, 0)$ is determined by the smallest eigenvalue, denoted by $\lambda_u(\alpha, \mu, \nu)$, of the linear problem

$$\nu \Delta \psi + (m - \tilde{u})\psi = -\lambda \psi \quad \text{in } \Omega, \qquad \nabla \psi \cdot n|_{\partial\Omega} = 0.$$

We first recall the following result [9] concerning the profile of $\tilde{u}$ for sufficiently large α.

Lemma 3.1. *For any positive solution $\tilde{u}$ of (3.1), $\tilde{u} \to m_+$ weakly in H^1 and strongly in L^2 as $\alpha/\mu \to \infty$. Furthermore, for any given $\eta > 0$, if $\alpha \geqslant \eta$ and $\alpha/\mu \to \infty$, $\tilde{u} \to m_+$ in $C^\gamma(\overline{\Omega})$ for some $\gamma \in (0, 1)$.*

If one further assumes that $m > 0$ in $\overline{\Omega}$, then for any given $\eta > 0$, if $\alpha \geqslant \eta$ and $\alpha/\mu \to \infty$, then $\tilde{u} \to m$ in $C^2(\overline{\Omega})$. Moreover,

(1) *if $\alpha/\mu \to \infty$ and $\alpha \to \infty$, we have*

$$\frac{\alpha}{\mu}(\tilde{u} - m) \to \frac{\int_\Omega m \ln m}{\int_\Omega m} - \ln m \tag{3.2}$$

uniformly in $\overline{\Omega}$;

(2) *if $\alpha/\mu \to \infty$ and $\alpha \to \tilde{\alpha} \in (0, \infty)$, then*

$$\frac{\alpha}{\mu}(\tilde{u} - m) \to \tilde{w} - \ln m, \tag{3.3}$$

uniformly in $\overline{\Omega}$, where $\tilde{w}$ is the unique solution of

$$\tilde{\alpha} \Delta \tilde{w} + \tilde{\alpha} \nabla \tilde{w} \cdot \nabla(\ln m) = \tilde{w} - \ln m \quad \text{in } \Omega, \qquad \frac{\partial \tilde{w}}{\partial n} = 0 \quad \text{on } \partial\Omega. \tag{3.4}$$

The following two results will play important roles in later analysis.

Lemma 3.2. *Suppose that $m > 0$ in $\overline{\Omega}$. Then*

$$\int_\Omega m \cdot \ln m \geqslant \frac{\int_\Omega m \cdot \int_\Omega \ln m}{|\Omega|}, \tag{3.5}$$

and equality holds if and only if m is a constant function.

Proof. We first make the following claim: For any continuous function g,

$$\int_\Omega (g-\bar{g})e^g \geqslant 0, \tag{3.6}$$

where the equality holds if and only if $g \equiv \bar{g}$, where $\bar{g} = \int_\Omega g/|\Omega|$.

To establish our assertion, for $\tau \in \mathbb{R}$, define

$$h(\tau) = \int_\Omega (g-\bar{g})e^{\tau(g-\bar{g})}.$$

Then,

$$\frac{dh}{d\tau} = \int_\Omega (g-\bar{g})^2 e^{\tau(g-\bar{g})} \geqslant 0$$

with equality if and only if $g \equiv \bar{g}$. Therefore, if $g \not\equiv \bar{g}$, we have $h(1) > h(0)$. Since $h(0) = 0$, we have

$$\int_\Omega (g-\bar{g})e^{g-\bar{g}} > 0,$$

which implies (3.6). This proves our assertion.

Rewrite (3.6) as

$$\int_\Omega g e^g \geqslant \frac{\int_\Omega g}{|\Omega|} \int_\Omega e^g.$$

Now choose $g = \ln m$, we see that (3.5) holds, and the inequality is strict if m is not a constant. This completes the proof. □

Lemma 3.3. *Suppose that $m > 0$ in $\overline{\Omega}$, m is a non-constant function. Then, for $\tilde{w}$ given by (3.4),*

$$\int_\Omega (\tilde{w} - \ln m)\, dx > 0. \tag{3.7}$$

Proof. Rewrite the equation of $\tilde{w}$ as

$$\tilde{\alpha}\nabla \cdot [m\nabla \tilde{w}] = m[\tilde{w} - \ln m] \quad \text{in } \Omega, \qquad \frac{\partial \tilde{w}}{\partial n} = 0 \quad \text{on } \partial\Omega. \tag{3.8}$$

Multiplying the above equation by $e^{-\tilde{w}}$ and integrating the result in Ω, we have

$$\int_\Omega m e^{-\tilde{w}}[\tilde{w} - \ln m] = \tilde{\alpha}\int_\Omega m e^{-\tilde{w}}|\nabla \tilde{w}|^2 > 0,$$

where the last inequality is strict since $\tilde{w}$ is non-constant as m is non-constant. In particular,

$$\int_{\Omega} e^{-[\tilde{w}-\ln m]}[\tilde{w}-\ln m] > 0. \tag{3.9}$$

Given any η, define the function $F(\eta)$ by

$$F(\eta) = \int_{\Omega} e^{-\eta(\tilde{w}-\ln m)}(\tilde{w}-\ln m).$$

Since

$$F'(\eta) = -\int_{\Omega} e^{-\eta(\tilde{w}-\ln m)}(\tilde{w}-\ln m)^2 \leqslant 0,$$

we have $F(1) \leqslant F(0)$, i.e.,

$$\int_{\Omega} (\tilde{w}-\ln m) = F(0) \geqslant F(1) = \int_{\Omega} e^{-(\tilde{w}-\ln m)}(\tilde{w}-\ln m). \tag{3.10}$$

It is clear that (3.7) follows from (3.9) and (3.10). $\square$

Proof of Theorem 3. We argue by contradiction. Suppose that there exists $\eta_0 > 0$ such that, passing to some sequence if necessary, for $\alpha \geqslant \eta_0$ and $\alpha/\mu \to \infty$, the smallest eigenvalue (denoted by γ_1) of the linear eigenvalue problem

$$-\nu\Delta\psi + \psi(-m+\tilde{u}) = \gamma\psi \quad \text{in } \Omega, \qquad \frac{\partial\psi}{\partial n} = 0 \quad \text{on } \partial\Omega$$

is non-positive. We choose the corresponding eigenfunction ψ_1 such that $\psi_1 > 0$ in $\overline{\Omega}$ and $\|\psi_1\|_\infty = 1$. Without loss of generality, we may assume that either $\alpha \to \infty$ or $\alpha \to \tilde{\alpha} \in (0, \infty)$. Since $0 \leqslant \tilde{u} \leqslant \max_{\overline{\Omega}} m$ [9, Corollary 3.2], we see that $|\gamma_1|$ is uniformly bounded, i.e., $|\gamma_1| \leqslant C$ for some positive constant C which is independent of μ and α. Since $\tilde{u}$ and ψ_1 are uniformly bounded, by standard elliptic regularity [22] we see that $\|\psi_1\|_{W^{2,p}(\Omega)}$ is uniformly bounded for any $p > 1$. By Sobolev's embedding theorem [22] and $\|\tilde{u} - m_+\|_2 \to 0$ (Lemma 3.1), we may assume that $\psi_1 \to \Psi$ in C^1, where Ψ is a weak solution of

$$-\nu\Delta\Psi + (-m+m_+)\Psi = \Lambda\Psi \quad \text{in } \Omega, \qquad \frac{\partial\Psi}{\partial n} = 0 \quad \text{on } \partial\Omega,$$

$\Psi \geqslant 0$ in $\overline{\Omega}$, and $\|\Psi\|_\infty = 1$. Note that $\Lambda \leqslant 0$ since $\gamma_1 \leqslant 0$. There are three cases for our consideration.

Case 1. *m changes sign*. For this case, $m - m_+$ is non-positive and non-trivial. Hence, $\Lambda > 0$, which is a contradiction.

Case 2. *$m > 0$ in $\overline{\Omega}$, $\alpha \to \infty$ and $\alpha/\mu \to \infty$*. Since $\|\psi_1\|_\infty = 1$ and $m - m_+ \equiv 0$, we see that $\Psi \equiv 1$, i.e., $\psi_1 \to 1$. Integrating the equation of ψ_1 in Ω, we have

$$\gamma_1 \int_{\Omega} \psi_1 = \int_{\Omega} \psi_1(\tilde{u} - m). \tag{3.11}$$

Since $\psi_1 \to 1$ uniformly and $(\alpha/\mu)(\tilde{u}-m) \to \int_\Omega m\ln m / \int_\Omega m - \ln m$ (Lemma 3.1), we have

$$\lim_{\alpha/\mu,\alpha\to\infty} \frac{\gamma_1\alpha}{\mu} = \left[\frac{\int_\Omega m\ln m}{\int_\Omega m} - \frac{\int_\Omega \ln m}{|\Omega|}\right] > 0,$$

where the last inequality follows from Lemma 3.2. In particular, $\gamma_1 > 0$ for sufficiently large α and α/μ, which is again a contradiction.

Case 3. *$m > 0$ in $\overline{\Omega}$, $\alpha/\mu \to \infty$ and $\alpha \to \tilde{\alpha} > 0$.* As in the previous case, we have $\psi_1 \to 1$ uniformly, and $(\alpha/\mu)(\tilde{u}-m) \to \tilde{w} - m$ (Lemma 3.1), where $\tilde{w}$ is the unique solution of (3.4). Therefore,

$$\lim_{\alpha/\mu\to\infty,\,\alpha\to\tilde{\alpha}} \frac{\lambda_1\alpha}{\mu}|\Omega| = \lim_{\alpha/\mu\to\infty,\,\alpha\to\tilde{\alpha}} \int_\Omega \frac{\alpha}{\mu}(\tilde{u}-m) = \int_\Omega (\tilde{w} - \ln m) > 0,$$

where the last inequality follows from Lemma 3.3, again a contradiction. □

4. Stability of $(0, \theta)$

This section is devoted to the proofs of Theorems 4 and 6. Theorem 4 is proved in Lemma 4.2, and Theorem 6 is a consequence of Theorems 2 and 10.

Recall that θ is a positive solution of

$$\nu\Delta\theta + \theta(m-\theta) = 0 \quad \text{in } \Omega, \qquad \nabla\theta\cdot n|_{\partial\Omega} = 0, \tag{4.1}$$

and it is unique whenever it exists. The stability of $(0,\theta)$ is determined by the smallest eigenvalue, denoted by $\lambda_v(\alpha,\mu,\nu)$, of the linear problem

$$\begin{cases} \nabla\cdot\left[\mu\nabla\varphi - \alpha\varphi\nabla(m-\theta)\right] + \varphi[m-\theta] = -\lambda\varphi & \text{in } \Omega, \\ \left[\mu\nabla\varphi - \alpha\varphi\nabla(m-\theta)\right]\cdot n|_{\partial\Omega} = 0. \end{cases} \tag{4.2}$$

Define

$$F(\eta) = \int_\Omega e^{\eta(m-\theta)}(m-\theta), \quad \eta \geqslant 0.$$

Lemma 4.1. *There exists a unique $\eta^* > 0$ such that $F(\eta) > 0$ if $\eta > \eta^*$ and $F(\eta) < 0$ if $\eta < \eta^*$.*

Proof. The proof was essentially given in Proposition 2.1 of [18]. Since

$$F'(\eta) = \int_\Omega e^{\eta(m-\theta)}(m-\theta)^2 > 0,$$

so F has at most one root. Note that

$$F(0) = \int_\Omega (m-\theta) = -\nu\int_\Omega \frac{\Delta\theta}{\theta} = -\nu\int_\Omega \frac{|\nabla\theta|^2}{\theta^2} < 0.$$

Since $m-\theta$ is positive somewhere in Ω, we see that $\lim_{\eta\to\infty} F(\eta) = +\infty$. Hence, $F(\eta) = 0$ has exactly one positive root, denoted by η^*. In particular, $F(\eta) > 0$ if $\eta > \eta^*$ and $F(\eta) < 0$ if $\eta < \eta^*$. □

Lemma 4.2. *If $\alpha/\mu > \eta^*$, then $\lambda_\nu(\alpha,\mu,\nu) < 0$, i.e., $(0,\theta)$ is linearly unstable.*

Proof. Set $\rho = e^{-(\alpha/\mu)(m-\theta)}\varphi$ in (4.2). Then ρ satisfies

$$\begin{cases} \mu\nabla\cdot\left[e^{(\alpha/\mu)(m-\theta)}\nabla\rho\right] + e^{(\alpha/\mu)(m-\theta)}(m-\theta)\rho = -\lambda_\nu(\alpha,\mu,\nu)e^{(\alpha/\mu)(m-\theta)}\rho \quad \text{in } \Omega, \\ \nabla\rho\cdot n|_{\partial\Omega} = 0. \end{cases} \tag{4.3}$$

Dividing the first equation in (4.3) by ρ and integrating in Ω, we see that

$$\begin{aligned} \lambda_\nu(\alpha,\mu,\nu)\int_\Omega e^{(\alpha/\mu)(m-\theta)} &= -\int_\Omega e^{(\alpha/\mu)(m-\theta)}(m-\theta) - \mu\int_\Omega \frac{\nabla\cdot[e^{(\alpha/\mu)(m-\theta)}\nabla\rho]}{\rho} \\ &= -F\left(\frac{\alpha}{\mu}\right) - \mu\int_\Omega e^{(\alpha/\mu)(m-\theta)}\frac{|\nabla\rho|^2}{\rho^2} \\ &< -F\left(\frac{\alpha}{\mu}\right) \\ &< -F\left(\eta^*\right) = 0, \end{aligned}$$

where the last inequality follows from assumption $\alpha/\mu > \eta^*$ and Lemma 4.1. □

The following result shows that under suitable conditions λ_ν is strictly monotone in α:

Theorem 10. *Suppose that Ω is convex and the Hessian matrix of $m(x)$ is negative definite for every $x \in \overline{\Omega}$. Then there exists some $\nu_0 > 0$ such that if $\nu > \nu_0$, then λ_ν is strictly monotone decreasing for all $\alpha \geqslant 0$.*

Set

$$V(x) := m - \theta.$$

By (4.3), $\rho > 0$ also satisfies

$$\mu\Delta\rho + \alpha\nabla V\cdot\nabla\rho + V\rho + \lambda_\nu\rho = 0 \quad \text{in } \Omega, \qquad \left.\frac{\partial\rho}{\partial n}\right|_{\partial\Omega} = 0. \tag{4.4}$$

Lemma 4.3. *For any $\alpha \geqslant 0$,*

$$\frac{\partial\lambda_\nu}{\partial\alpha} = -\frac{\int_\Omega e^{(\alpha/\mu)V}\rho\nabla\rho\cdot\nabla V}{\int_\Omega e^{(\alpha/\mu)V}\rho^2}. \tag{4.5}$$

Proof. In the following we denote $\partial\rho/\partial\alpha$ by ρ' and similarly for λ_ν'. Differentiating (4.4) with respect to α, we have

$$\mu\Delta\rho' + \nabla V\cdot\nabla\rho + \alpha\nabla V\cdot\nabla\rho' + V\rho' + \lambda_\nu'\rho + \lambda_\nu\rho' = 0, \qquad \left.\frac{\partial\rho'}{\partial n}\right|_{\partial\Omega} = 0. \tag{4.6}$$

Rewrite (4.6) as

$$\begin{cases} \mu\nabla\cdot\left[e^{(\alpha/\mu)V}\nabla\rho'\right]+e^{(\alpha/\mu)V}\nabla V\cdot\nabla\rho+e^{(\alpha/\mu)V}V\rho'+\lambda_v'\rho e^{(\alpha/\mu)V}+\lambda_v e^{(\alpha/\mu)V}\rho'=0, \\ \left.\dfrac{\partial\rho'}{\partial n}\right|_{\partial\Omega}=0. \end{cases} \tag{4.7}$$

Multiplying (4.7) by ρ, (4.3) by ρ', subtracting and integrating in Ω, we find that (4.5) holds. □

It is clear that Theorem 10 follows from Lemma 4.3 and the following result.

Proposition 5. *Suppose that Ω is convex and the Hessian matrix of $m(x)$ is negative definite for every $x\in\overline{\Omega}$. Then there exists some $\nu_0>0$ such that if $\nu>\nu_0$,*

$$\int_\Omega e^{(\alpha/\mu)V}\rho\nabla\rho\cdot\nabla V>0$$

for every $\alpha\geqslant 0$ and every $\mu>0$.

To establish Proposition 5, we first prove the following lemma.

Lemma 4.4. *The following holds*:

$$\int_\Omega e^{(\alpha/\mu)V}\rho\nabla\rho\nabla V=\int_\Omega e^{(\alpha/\mu)V}\left[\mu\left|\nabla^2\rho\right|^2-V|\nabla\rho|^2-\lambda_v|\nabla\rho|^2\right]$$
$$-\frac{\mu}{2}\int_{\partial\Omega}e^{(\alpha/\mu)V}\frac{\partial}{\partial n}|\nabla\rho|^2-\alpha\int_\Omega e^{(\alpha/\mu)V}(\nabla\rho)^T\cdot\nabla^2V\cdot\nabla\rho. \tag{4.8}$$

Proof. Differentiate (4.4) with respect to x_i and write the result in vector form:

$$\mu\Delta(\nabla\rho)+\alpha\nabla^2V\cdot\nabla\rho+\alpha\nabla^2\rho\cdot\nabla V+\rho\nabla V+V\nabla\rho+\lambda_v\nabla\rho=0, \tag{4.9}$$

where ∇^2V denotes the symmetric matrix $(V_{x_ix_j})$, i.e. the Hessian of V. Multiplying (4.9) by $e^{(\alpha/\mu)V}\nabla\rho$ (take inner product of vectors) and integrating the result in Ω we have

$$\begin{aligned}&\int_\Omega e^{(\alpha/\mu)V}\rho\nabla\rho\cdot\nabla V\\ &=-\lambda_v\int_\Omega e^{(\alpha/\mu)V}|\nabla\rho|^2-\mu\int_\Omega e^{(\alpha/\mu)V}\nabla\rho\cdot\Delta(\nabla\rho)-\alpha\int_\Omega e^{(\alpha/\mu)V}(\nabla\rho)^T\cdot\nabla^2V\cdot\nabla\rho\\ &\quad-\alpha\int_\Omega e^{(\alpha/\mu)V}(\nabla\rho)^T\cdot\nabla^2\rho\cdot\nabla V-\int_\Omega e^{(\alpha/\mu)V}V|\nabla\rho|^2.\end{aligned} \tag{4.10}$$

Multiplying the identity

$$\left|\nabla^2\rho\right|^2+\nabla(\Delta\rho)\cdot\nabla\rho=\frac{1}{2}\Delta\left(|\nabla\rho|^2\right)$$

by $e^{(\alpha/\mu)V}$ and integrating the result in Ω, we have

$$\int_\Omega e^{(\alpha/\mu)V}\nabla(\Delta\rho)\cdot\nabla\rho$$
$$= -\int_\Omega e^{(\alpha/\mu)V}\left|\nabla^2\rho\right|^2 + \frac{1}{2}\int_{\partial\Omega} e^{(\alpha/\mu)V}\frac{\partial}{\partial n}|\nabla\rho|^2 - \frac{\alpha}{\mu}\int_\Omega e^{(\alpha/\mu)V}(\nabla V)^T\cdot\nabla^2\rho\cdot\nabla\rho. \quad (4.11)$$

Hence, Eq. (4.8) follows from Eqs. (4.10) and (4.11). □

Lemma 4.5. *The following holds*:

$$\int_\Omega e^{(\alpha/\mu)V}\left[\mu\left|\nabla^2\rho\right|^2 - V|\nabla\rho|^2 - \lambda_v|\nabla\rho|^2\right] \geqslant 0. \quad (4.12)$$

Proof. By (4.3), λ_v can be characterized as

$$\lambda_v = \inf_{\psi\in W^{1,2}(\Omega)} \frac{\int_\Omega e^{(\alpha/\mu)V}[\mu|\nabla\psi|^2 - V\psi^2]}{\int_\Omega \psi^2}.$$

Choosing the test function $\psi = \rho_{x_i}$ for every $1 \leqslant i \leqslant n$, we have

$$\int_\Omega e^{(\alpha/\mu)V}\left[\mu|\nabla\rho_{x_i}|^2 - V|\rho_{x_i}|^2 - \lambda_v|\rho_{x_i}|^2\right] \geqslant 0,$$

and summing up i from 1 to N, we see that (4.12) holds. □

The following result belongs to Casten and Holland [12] and Matano [41].

Lemma 4.6. *Suppose that Ω is convex. Then*

$$\frac{\partial}{\partial n}|\nabla\rho|^2 \leqslant 0$$

on $\partial\Omega$.

Proof of Proposition 5. By Eqs. (4.8) and (4.12) and Lemma 4.6,

$$\int_\Omega e^{(\alpha/\mu)V}\rho\nabla\rho\cdot\nabla V \geqslant -\alpha\int_\Omega e^{(\alpha/\mu)V}(\nabla\rho)^T\cdot\nabla^2 V\cdot\nabla\rho. \quad (4.13)$$

As $\theta \to \frac{1}{|\Omega|}\int_\Omega m$ in $C^2(\overline{\Omega})$ when $\nu\to\infty$ and $\nabla^2 m$ is negative definite for every $x\in\overline{\Omega}$, there exists some $\nu_0 > 0$ such that if $\nu > \nu_0$, $\nabla^2 V = \nabla^2 m - \nabla^2\theta$ is negative definite for every $x\in\overline{\Omega}$. This completes the proof of Proposition 5. □

5. Non-existence of positive steady states for large α

This section is devoted to the proof of Theorem 5, which is a corollary of Lemma 5.5. To this end, we first establish a few auxiliary results.

Lemma 5.1. *For any componentwise non-negative equilibrium (u, v) of (1.4), $u(x) \leqslant \max_{\overline{\Omega}} m$ for every $x \in \overline{\Omega}$.*

Proof. Set

$$w = ue^{-(\alpha/\mu)f(x,u+v)}. \tag{5.1}$$

Then w satisfies zero Neumann boundary condition and

$$\mu\nabla\cdot\left[e^{(\alpha/\mu)f}\nabla w\right] + uf(x,u+v) = 0 \quad \text{in } \Omega. \tag{5.2}$$

Let $w(x_\alpha) = \max_{\overline{\Omega}} w$ for some $x_\alpha \in \overline{\Omega}$. Rewrite the equation of w as

$$\mu\Delta w + \alpha\nabla m\cdot\nabla w + wf(x,u+v) = 0 \quad \text{in } \Omega.$$

Then by the maximum principle (cf. [39, Lemma 2.1]),

$$m(x_\alpha) - u(x_\alpha) - v(x_\alpha) \geqslant 0. \tag{5.3}$$

By (5.3) we have

$$\begin{aligned}\max_{\overline{\Omega}} w = w(x_\alpha) &= e^{-(\alpha/\mu)[m(x_\alpha)-u(x_\alpha)-v(x_\alpha)]}u(x_\alpha)\\ &\leqslant u(x_\alpha)\\ &\leqslant m(x_\alpha)\\ &\leqslant \max_{\overline{\Omega}} m.\end{aligned} \tag{5.4}$$

By the definition of w, we have

$$u(x)e^{-(\alpha/\mu)[m(x)-u(x)-v(x)]} \leqslant \max_{\overline{\Omega}} m \tag{5.5}$$

for every $x \in \overline{\Omega}$. If $u(\tilde{x}) > \max_{\overline{\Omega}} m$ for some $\tilde{x}$, then $m(\tilde{x}) < u(\tilde{x})$. This along with (5.5) implies that

$$u(\tilde{x}) \leqslant u(\tilde{x})e^{-(\alpha/\mu)[m(\tilde{x})-u(\tilde{x})-v(\tilde{x})]} \leqslant \max_{\overline{\Omega}} m,$$

which contradicts our assumption $u(\tilde{x}) > \max_{\overline{\Omega}} m$. Hence, $\max_{\overline{\Omega}} u \leqslant \max_{\overline{\Omega}} m$. □

Lemma 5.2. *For any $p \geqslant 1$, $\|v\|_{W^{2,p}}$ is uniformly bounded for non-negative equilibria of (1.4) and for all $\alpha \geqslant 0$ and $\mu > 0$.*

Proof. By the maximum principle, $v(x) \leqslant \max_{\overline{\Omega}} m$ in $\overline{\Omega}$. By Lemma 5.1 and L^p estimates [22] we see that $\|v\|_{W^{2,p}}$ is uniformly bounded. □

Lemma 5.3. *For any positive steady state of* (1.4), $\|u\|_{H^1}$ *is uniformly bounded for all* $\alpha \geqslant 0$ *and* $\mu > 0$.

Proof. Multiplying the equation of u by $f(x, u+v)$ and integrating in Ω, we have

$$\mu \int_\Omega |\nabla u|^2 + \alpha \int_\Omega u|\nabla f|^2 + \int_\Omega uf^2 = \mu \int_\Omega \nabla u \cdot \nabla m - \mu \int_\Omega \nabla u \cdot \nabla v.$$

By Lemma 5.2 and Cauchy–Schwartz inequality we see that

$$\frac{\mu}{2} \int_\Omega |\nabla u|^2 + \alpha \int_\Omega u|\nabla f|^2 + \int_\Omega uf^2 \leqslant C\mu, \tag{5.6}$$

where $C > 0$ is some constant independent of α and μ. In particular, $\int_\Omega |\nabla u|^2 \leqslant C$. Since u is also uniformly bounded, this proves our assertion. □

Lemma 5.4. *For any positive equilibria of* (1.4),

$$\int_\Omega (m-u-v)_+ \leqslant \frac{\mu}{\alpha}|\Omega|. \tag{5.7}$$

Proof. Let w be defined as in (5.1). Dividing (5.2) by w and integrating in Ω, we find that

$$\int_\Omega e^{(\alpha/\mu)f} f = -\mu \int_\Omega \frac{e^{(\alpha/\mu)f}|\nabla w|^2}{w^2} \leqslant 0.$$

It is easy to check that $ye^{(\alpha/\mu)y} \geqslant (\alpha/\mu)y^2$ for $y \geqslant 0$, and $ye^{(\alpha/\mu)y} \geqslant -\mu/\alpha$ for every $y \in \mathbb{R}$. Hence,

$$0 \geqslant \int_{\{f \geqslant 0\}} e^{(\alpha/\mu)f} f + \int_{\{f<0\}} e^{(\alpha/\mu)f} f \geqslant \frac{\alpha}{\mu} \int_{\{f\geqslant 0\}} f^2 - \frac{\mu}{\alpha}|\Omega|.$$

Therefore,

$$\int_{\{f \geqslant 0\}} f^2 \leqslant \frac{\mu^2}{\alpha^2}|\Omega|.$$

By Hölder's inequality, we have

$$\int_\Omega f_+ \leqslant \left(\int_\Omega (f_+)^2\right)^{1/2} |\Omega|^{1/2} = \left(\int_{\{f\geqslant 0\}} f^2\right)^{1/2} |\Omega|^{1/2} \leqslant \frac{\mu}{\alpha}|\Omega|. \qquad \square$$

Lemma 5.5. *Suppose that* $m(x)$ *changes sign in* Ω. *For any* $\eta > 0$, *there exists some positive constant* $C = C(\eta)$ (*independent of* α, μ) *such that if* $\alpha \geqslant \eta$ *and* $\alpha/\mu \geqslant C$, *then system* (1.4) *has no positive equilibria.*

Proof. To prove the non-existence of positive equilibria, we argue by contradiction. Suppose that there exists $\eta_0 > 0$ such that $\alpha \geqslant \eta_0$, $\alpha/\mu \to \infty$, and (1.4) has positive steady states. By Lemmas 5.2 and 5.3 and Sobolev's embedding theorem [22] we may assume that as $\alpha/\mu \to \infty$, passing to a sequence if necessary, $u \to u^*$ weakly in H^1 and strongly in L^2, and $v \to v^*$ in $W^{2,p}$ weakly and strongly in $C^{1,\gamma}(\overline{\Omega})$ for some non-negative functions u^*, v^*, where $p \in (1,\infty)$ and $\gamma \in (0,1)$. By Lemmas 5.1 and 5.2, we see that $u^*, v^* \in L^\infty(\Omega)$. In particular, v^* is a non-negative weak solution of

$$\nu \Delta v^* + v^*\big(m - u^* - v^*\big) = 0 \quad \text{in } \Omega, \qquad \frac{\partial v^*}{\partial n} = 0 \quad \text{on } \partial\Omega. \tag{5.8}$$

Since $u^*, v^* \in L^\infty(\Omega)$, by elliptic regularity [22] we have $v^* \in W^{2,p}(\Omega) \cap C^{1,\gamma}(\overline{\Omega})$ for every $\gamma \in (0,1)$ and $p > 1$.

Passing to the limit in (5.7), we have

$$\int_\Omega \big(m - u^* - v^*\big)_+ = 0.$$

Since both u^* and v^* are non-negative functions, we have

$$u^*(x) + v^*(x) \geqslant m_+(x) \quad \text{a.e. in } \Omega. \tag{5.9}$$

We consider two different cases:

Case 1. $v^* \not\equiv 0$. For this case, by the strong maximum principle [43] we have $v^* > 0$ in Ω. By (5.9) we see that $m - u^* - v^* \leqslant 0$ in Ω and $m - u^* - v^* < 0$ in $\{x \in \Omega\colon\ m(x) < 0\}$. Hence,

$$\begin{aligned}\int_\Omega v^*\big(m - u^* - v^*\big) &= \int_{\{x\in\Omega:\ m(x)\geqslant 0\}} v^*\big(m - u^* - v^*\big) + \int_{\{x\in\Omega:\ m(x)<0\}} v^*\big(m - u^* - v^*\big) \\ &\leqslant \int_{\{x\in\Omega:\ m(x)<0\}} v^*\big(m - u^* - v^*\big) < 0.\end{aligned} \tag{5.10}$$

On the other hand, integrating (5.8) in Ω,

$$\int_\Omega v^*\big(m - u^* - v^*\big) = 0,$$

which contradicts (5.10).

Case 2. $v^* \equiv 0$. Hence, $v \to 0$ as $\alpha \to \infty$. Set $\tilde{v} = v/\|v\|_\infty$. Passing to a subsequence if necessary, by elliptic regularity and Sobolev's embedding theorem [22] we may assume that $\tilde{v} \to v^{**}$ in C^1, where v^{**} is a non-negative weak solution of

$$\nu \Delta v^{**} + v^{**}\big(m - u^*\big) = 0 \quad \text{in } \Omega, \qquad \nabla v^{**} \cdot n|_{\partial\Omega} = 0. \tag{5.11}$$

Since $v^* = 0$ a.e., we have $u^* \geqslant m_+$ a.e. in Ω. By the same argument as in Case 1, we see that the only non-negative solution of (5.11) is $v^{**} = 0$, which is a contradiction since $\|v^{**}\|_\infty = 1$. This proves that system (1.4) has no positive equilibria when m changes sign. $\square$

6. Existence of positive steady state: Bifurcation approach

This section is devoted to the proof of Theorem 7. The local bifurcation result is a consequence of Theorem 11 and Lemmas 6.1, 6.2 and 6.3. The global bifurcation part is established at the end of this section.

6.1. Local bifurcation

We first state a version of the well-known local bifurcation theorem of Crandall and Rabinowitz [19] from simple eigenvalues. We will also use a recent result by Shi and Wang [44] that provides a global bifurcation result under the hypotheses of the local bifurcation theorem together with some additional conditions. Let X and Y be two Banach spaces.

Theorem 11. *Let V be an open connected subset of $\mathbb{R} \times X$ and $(\lambda_0, x_0) \in V$. Let F be a continuously differentiable mapping from V into Y. Suppose that*

1. *$F(\lambda, x_0) = 0$ for $(\lambda, x_0) \in V$.*
2. *$D_{\lambda x}F(\lambda, x)$ exists and is continuous in some neighborhood of (λ_0, x_0).*
3. *Both the kernel and co-kernel of $D_xF(\lambda_0, x_0)$, where $N(D_xF(\lambda_0, x_0))$ denote the kernel of $D_xF(\lambda_0, x_0)$ are one-dimensional and the range $R(D_xF(\lambda_0, x_0))$ is closed.*
4. *$D_{\lambda x}F(\lambda, x)(w_0) \notin R(D_xF(\lambda_0, x_0))$, where w_0 spans $N(D_xF(\lambda_0, x_0))$.*

Let Z be any complement of $N(D_xF(\lambda_0, x_0))$ in X. Then there exists some $\epsilon > 0$ and continuous functions $\lambda : (-\epsilon, \epsilon) \to \mathbb{R}$ and $\xi : (-\epsilon, \epsilon) \to Z$ such that $\lambda(0) = 0$ and $\xi(0) = 0$ and $F(\lambda(s), x_0 + sw_0 + s\xi(s)) = 0$, $s \in (-\epsilon, \epsilon)$. Moreover, the set $F^{-1}(0) = 0$ near (λ_0, x_0) consists of precisely the curves $\{(\lambda, x_0)\}$ and $\{(\lambda(s), x_0 + sw_0 + s\xi(s)),\ s \in (-\epsilon, \epsilon)\}$.

For the case $\Omega \subset \mathbb{R}^N$ we require $\partial\Omega$ to be of class C^3 and define

$$X = W^{2,p}(\Omega) \times W^{2,p}(\Omega),$$

$$Y = L^p(\Omega) \times L^p(\Omega) \times W^{1-1/p,p}(\partial\Omega) \times W^{1-1/p,p}(\partial\Omega),$$

$$V = \left\{(\alpha, u, v) \in (\delta, 1/\delta) \times X\colon\ u > -\frac{\mu}{2\alpha},\ v > -\delta\right\},$$

where $p > N$, $\delta > 0$ is small. Recall that for $p > N$, $W^{2,p}(\Omega)$ embeds in $C^{1,\gamma}(\overline{\Omega})$.

For the local bifurcation analysis we could replace X and Y with $\tilde{X} = C^{2,\gamma}(\overline{\Omega}) \times C_N^{2,\gamma}(\overline{\Omega})$, where $C_N^{2,\gamma}(\overline{\Omega}) := \{u \in C^{2,\gamma}(\overline{\Omega})\colon\ \nabla u \cdot n|_{\partial\Omega} = 0\}$ and $\tilde{Y} = C^{\gamma}(\overline{\Omega}) \times C^{\gamma}(\overline{\Omega}) \times C^{1,\gamma}(\partial\Omega)$. However, we will need to work in Sobolev spaces so that we can use the results of [44] for the global bifurcation analysis.

Define $F(\alpha, u, v) = (F_1, F_2, F_3, F_4)$, where

$$F_1(\alpha, u, v) = \nabla \cdot \left[\mu\nabla u - \alpha u \nabla f(x, u + v)\right] + uf(x, u + v),$$

$$F_2(\alpha, u, v) = \nu\Delta v + vf(x, u + v),$$

$$F_3(\alpha, u, v) = \left[\mu\nabla u - \alpha u \nabla f(x, u + v)\right] \cdot n,$$

$$F_4(\alpha, u, v) = \nu\nabla v \cdot n.$$

Since we take $p > N$ it is clear that F is smooth. By a direct calculation,

$$D_{(u,v)}F|_{(\alpha,u,v)=(\alpha,0,\theta)}(\varphi,\psi)=\begin{pmatrix}\nabla\cdot[\mu\nabla\varphi-\alpha\varphi\nabla(m-\theta)]+\varphi(m-\theta)\\ \nu\Delta\psi+\psi(m-2\theta)-\theta\varphi\\ [\mu\nabla\varphi-\alpha\varphi\nabla(m-\theta)]\cdot n\\ \nu\nabla\psi\cdot n\end{pmatrix}.$$

Lemma 6.1. *Suppose that Ω is convex and the Hessian matrix of m is negative definite for every $x\in\overline{\Omega}$. There exists some $\nu_0=\nu_0(m,\Omega)>0$ such that if $\nu>\nu_0$, $D_{(u,v)}F|_{(\alpha,0,\theta)}$ is invertible for any $\alpha<\alpha^*$, and at $\alpha=\alpha^*$, $N(D_{(u,v)}F|_{(\alpha^*,0,\theta)})$ is one-dimensional.*

Proof. $(\varphi,\psi)\in N(D_{(u,v)}F|_{(\alpha,0,\theta)})$ if and only if the linear problem

$$\begin{cases}\nabla\cdot\big[\mu\nabla\varphi-\alpha\varphi\nabla(m-\theta)\big]+\varphi(m-\theta)=0 & \text{in }\Omega,\\ \nu\Delta\psi+\psi(m-2\theta)-\theta\varphi=0 & \text{in }\Omega,\\ \big[\mu\nabla\varphi-\alpha\varphi\nabla(m-\theta)\big]\cdot n=\nabla\psi\cdot n=0 & \text{on }\partial\Omega\end{cases}$$

has non-trivial solution. By Theorem 6, we see that if $\alpha<\alpha^*$, the problem

$$\begin{cases}\nabla\cdot\big[\mu\nabla\varphi-\alpha\varphi\nabla(m-\theta)\big]+\varphi(m-\theta)=0 & \text{in }\Omega,\\ \big[\mu\nabla\varphi-\alpha\varphi\nabla(m-\theta)\big]\cdot n=0 & \text{on }\partial\Omega\end{cases}$$

has only the trivial solution $\varphi=0$. Hence, ψ satisfies

$$\nu\Delta\psi+\psi(m-2\theta)=0\quad\text{in }\Omega,\qquad\nabla\psi\cdot n=0\quad\text{on }\partial\Omega.$$

Since the operator $\nu\Delta\psi+\psi(m-2\theta)$ with zero Neumann boundary conditions is invertible, we see that $\psi=0$. Hence, if $\alpha<\alpha^*$, $D_{(u,v)}F|_{(\alpha,0,\theta)}$ is invertible.

For $\alpha=\alpha^*$, the problem

$$\begin{cases}\nabla\cdot\big[\mu\nabla\varphi-\alpha^*\varphi\nabla(m-\theta)\big]+\varphi(m-\theta)=0 & \text{in }\Omega,\\ \big[\mu\nabla\varphi-\alpha^*\varphi\nabla(m-\theta)\big]\cdot n=0 & \text{on }\partial\Omega\end{cases}\tag{6.1}$$

has a positive solution, denoted by φ^*, which is uniquely determined by $\max_{\overline{\Omega}}\varphi^*=1$. Since the operator $\nu\Delta\psi+\psi(m-2\theta)$ is invertible, we see that

$$N(D_{(u,v)}F|_{(\alpha^*,0,\theta)})=span\big(\varphi^*,\psi^*\big),$$

where ψ^* is the unique solution of

$$\nu\Delta\psi^*+\psi^*(m-2\theta)-\theta\varphi^*=0\quad\text{in }\Omega,\qquad\nabla\psi^*\cdot n=0\quad\text{on }\partial\Omega.$$

This completes the proof. □

Let $\rho>0$ be a principal eigenfunction of the adjoint problem of (6.1), i.e., ρ satisfies

$$\mu\Delta\rho+\alpha^*\nabla(m-\theta)\cdot\nabla\rho+(m-\theta)\rho=0\quad\text{in }\Omega,\qquad\nabla\rho\cdot n|_{\partial\Omega}=0,\tag{6.2}$$

or equivalently,

$$\mu\nabla\cdot\left[e^{(\alpha^*/\mu)(m-\theta)}\nabla\rho\right]+\rho e^{(\alpha^*/\mu)(m-\theta)}(m-\theta)=0 \quad \text{in } \Omega, \qquad \nabla\rho\cdot n|_{\partial\Omega}=0. \tag{6.3}$$

It is straightforward to check that

$$\rho = Ce^{-(\alpha^*/\mu)(m-\theta)}\varphi^*$$

for some positive constant C.

Lemma 6.2. *Suppose that Ω is convex and the Hessian matrix of m is negative definite for every $x \in \overline{\Omega}$. There exists some $\nu_0 = \nu_0(m, \Omega) > 0$ such that if $\nu > \nu_0$, then*

$$R(D_{(u,v)}F|_{(\alpha^*,0,\theta)}) = \left\{(h_1, h_2, g_1, g_2) \in Y\colon \int_\Omega h_1\rho = \int_{\partial\Omega} g_1\rho\right\}.$$

Proof. Given any $(h_1, h_2, g_1, g_2) \in Y$, $(h_1, h_2, g_1, g_2) \in R(D_{(u,v)}F|_{(\alpha^*,0,\theta)})$ if and only if there exist $(f_1, f_2) \in X$ such that $D_{(u,v)}F|_{(\alpha^*,0,\theta)}(f_1, f_2) = (h_1, h_2, g_1, g_2)$, which, due to the invertibility of the operator $\nu\Delta\psi + \psi(m - 2\theta)$, is equivalent to solving the equation

$$\begin{cases} \nabla\cdot\left[\mu\nabla f_1 - \alpha^* f_1\nabla(m-\theta)\right] + f_1(m-\theta) = h_1 & \text{in } \Omega, \\ \left[\mu\nabla f_1 - \alpha^* f_1\nabla(m-\theta)\right]\cdot n = g_1 & \text{on } \partial\Omega. \end{cases} \tag{6.4}$$

Set $\tilde f_1 = e^{-(\alpha^*/\mu)(m-\theta)} f_1$. Then (6.4) is equivalent to

$$\begin{cases} \mu\nabla\cdot\left[e^{(\alpha^*/\mu)(m-\theta)}\nabla\tilde f_1\right] + \tilde f_1 e^{(\alpha^*/\mu)(m-\theta)}(m-\theta) = h_1 & \text{in } \Omega, \\ \mu e^{(\alpha^*/\mu)(m-\theta)}(\nabla\tilde f_1\cdot n) = g_1 & \text{on } \partial\Omega. \end{cases} \tag{6.5}$$

By the Fredholm alternative for a single equation and (6.3), (6.5) is solvable if and only if $\int_\Omega h_1\rho = \int_{\partial\Omega} g_1\rho$. $\square$

Remark 6.1. It follows from the characterization of $R(D_{(u,v)}F|_{(\alpha^*,0,\theta)})$ in Lemma 6.2 that $R(D_{(u,v)}F|_{(\alpha^*,0,\theta)})$ is closed and has a one-dimensional complement, so Lemmas 6.1 and 6.2 imply that hypothesis 3 of Theorem 11 is satisfied and $D_{(u,v)}F|_{(\alpha^*,0,\theta)}$ is Fredholm.

Lemma 6.3. *Suppose that Ω is convex and the Hessian matrix of m is negative definite for every $x \in \overline{\Omega}$. There exists some $\nu_0 = \nu_0(m, \Omega) > 0$ such that if $\nu > \nu_0$, then $D_\alpha D_{(u,v)}F|_{(\alpha^*,0,\theta)}(\varphi^*, \psi^*) \notin R(D_{(u,v)}F|_{(\alpha^*,0,\theta)})$.*

Proof. From the proof of Lemma 6.1, $N(D_{(u,v)}F|_{(\alpha^*,0,\theta)})$ is one-dimensional and spanned by (φ^*, ψ^*). Hence,

$$D_\alpha D_{(u,v)}F|_{(\alpha^*,0,\theta)}(\varphi^*, \psi^*) = \begin{pmatrix} -\nabla\cdot[\varphi^*\nabla(m-\theta)] \\ 0 \\ -\varphi^*\nabla(m-\theta)\cdot n \\ 0 \end{pmatrix}.$$

From Lemma 6.2 we see that $D_\alpha D_{(u,v)} F|_{(\alpha^*,0,\theta)}(\varphi^*, \psi^*) \notin R(D_{(u,v)} F|_{(\alpha^*,0,\theta)})$ if and only if

$$\int_\Omega \rho \nabla \cdot \big(\varphi^* \nabla(m-\theta)\big) - \int_{\partial\Omega} \rho \varphi^* \nabla(m-\theta) \cdot n \neq 0. \tag{6.6}$$

Since

$$\begin{aligned}\int_{\partial\Omega} \rho \varphi^* \nabla(m-\theta) \cdot n &= \int_\Omega \nabla \cdot \big(\rho \varphi^* \nabla(m-\theta)\big) \\ &= \int_\Omega \varphi^* \nabla \rho \cdot \nabla(m-\theta) + \int_\Omega \rho \nabla \cdot \big[\varphi^* \nabla(m-\theta)\big],\end{aligned}$$

(6.6) is equivalent to

$$\int_\Omega \varphi^* \nabla \rho \cdot \nabla(m-\theta) \neq 0. \tag{6.7}$$

Since $\varphi^* = \rho e^{(\alpha^*/\mu)(m-\theta)}/C$ for some positive constant C, (6.7) is equivalent to

$$\int_\Omega e^{(\alpha^*/\mu)(m-\theta)} \rho \nabla \rho \cdot \nabla(m-\theta) \neq 0,$$

which holds due to Proposition 5. □

Remark 6.2. Lemmas 6.1, 6.2 and 6.3 verify the hypotheses of Theorem 11 and hence prove the local bifurcation result (1) in Theorem 7.

6.2. Global bifurcation

The paper [44] by Shi and Wang gives conditions under which the hypotheses of Theorem 11 imply a global bifurcation result. The following result is a combination of Theorems 4.3 and 4.4 of [44].

Theorem 12. *Suppose that the hypotheses of Theorem 11 are satisfied and that in addition*

1. *$D_x F(\lambda, x)$ exists and is Fredholm for all $(\lambda, x) \in V$, and $D_x F(\lambda, x_0)$ is continuously differentiable with respect to λ for all $(\lambda, x_0) \in V$,*
2. *the norm function $x \mapsto \|x\|$ on X is continuously differentiable for any $x \neq 0$, and*
3. *if $(\lambda, x), (\lambda, x_0) \in V$ then for any $k \in (0,1)$, the operator $kD_x F(\lambda, x) + (1-k) D_x F(\lambda, x_0)$ is Fredholm.*

Let $\Gamma^+ = \{(\lambda(s), x_0 + sw_0 + s\xi(s)),\ s \in (0, \epsilon)\}$ and $\Gamma^- = \{(\lambda(s), x_0 + sw_0 + s\xi(s)),\ s \in (-\epsilon, 0)\}$. Then Γ^+ and Γ^- are contained in $\mathcal{C}$, where $\mathcal{C}$ is a connected component of $\overline{S}$ with $S = \{(\lambda, x) \in V\colon\ F(\lambda, x) = 0,\ x \neq x_0\}$. Let $\mathcal{C}^+$ be the connected component of $\mathcal{C} \backslash \Gamma^-$ containing Γ^+ and let $\mathcal{C}^-$ be the connected component of $\mathcal{C} \backslash \Gamma^+$ containing Γ^-. Each of $\mathcal{C}^+$ and $\mathcal{C}^-$ satisfies one of the following: (i) *it is not compact in V,* (ii) *it contains a point (λ_*, x_0) with $\lambda_* \neq \lambda_0$, or* (iii) *it contains a point $(\lambda, x_0 + z)$ where $z \neq 0$ and $z \in Z$, where Z is as in Theorem 11.*

We first establish two auxiliary results.

Lemma 6.4. *Given any $\Lambda > 0$, there exist some positive constants $C := C(\Lambda)$ and $\gamma := \gamma(\Lambda) \in (0,1)$ such that for any positive steady states of (1.4) with $0 \leqslant \alpha \leqslant \Lambda$, $\|u\|_{C^{2,\gamma}(\Omega)} \leqslant C$ and $\|v\|_{C^{2,\gamma}(\Omega)} \leqslant C$.*

Proof. Since $\|u\|_{L^\infty}$ and $\|v\|_{L^\infty}$ are bounded (Lemmas 5.1 and 5.2), by elliptic regularity theory [22] we see that for any $p > 1$, $\|v\|_{W^{2,p}(\Omega)}$ is uniformly bounded for $\alpha \geqslant 0$. By the Sobolev embedding theorem [22], $\|v\|_{C^{1,\tau}(\Omega)}$ is uniformly bounded for $\alpha \geqslant 0$ and any $\tau \in (0,1)$. Set $w = e^{-(\alpha/\mu) f(x,u+v)} u$. Then w satisfies

$$\mu \nabla \cdot \left[e^{(\alpha/\mu) f(x,u+v)} \nabla w\right] + u(m-u-v) = 0 \quad \text{in } \Omega, \qquad \frac{\partial w}{\partial n} = 0 \quad \text{on } \partial\Omega. \tag{6.8}$$

Since $\|u\|_{L^\infty}$ and $\|v\|_{L^\infty}$ are bounded, f and w are bounded for $0 \leqslant \alpha \leqslant \Lambda$. By De Giorgi–Nash estimate up to the boundary (cf. [37, Lemma 5.1]; [36, Theorem 6.44]), there exists some $\gamma \in (0,1)$ such that $\|w\|_{C^\gamma(\overline{\Omega})}$ is uniformly bounded for $0 \leqslant \alpha \leqslant \Lambda$. Define $h(y) = e^{(\alpha/\mu)y} y$. Note that $h(u) = we^{(\alpha/\mu)(m-v)}$. As $\|w\|_{C^\gamma(\overline{\Omega})}$, $m \in C^2(\overline{\Omega})$ and $\|v\|_{C^1(\Omega)}$ are uniformly bounded, $\|h(u)\|_{C^\gamma(\overline{\Omega})}$ is uniformly bounded for $0 \leqslant \alpha \leqslant \Lambda$. Since h is smooth and $h'(y) > 0$ for $y > -\mu/\alpha$, we see that $\|u\|_{C^\gamma(\overline{\Omega})}$ is uniformly bounded for $0 \leqslant \alpha \leqslant \Lambda$. By the Schauder theory [22], $\|v\|_{C^{2,\gamma}(\overline{\Omega})}$ is uniformly bounded for $0 \leqslant \alpha \leqslant \Lambda$. Furthermore, $\|f(\cdot, u+v)\|_{C^\gamma(\overline{\Omega})}$ is uniformly bounded for $0 \leqslant \alpha \leqslant \Lambda$. By the Schauder theory for second elliptic operator with the divergence form (cf. [25, Theorem 2.8]), $\|w\|_{C^{1,\gamma}(\overline{\Omega})}$ is uniformly bounded for $0 \leqslant \alpha \leqslant \Lambda$. As $m \in C^2(\overline{\Omega})$ and $\|v\|_{C^{1,\gamma}(\Omega)}$ are uniformly bounded, $\|h(u)\|_{C^{1,\gamma}(\overline{\Omega})}$ is uniformly bounded, which in turn implies that $\|u\|_{C^{1,\gamma}(\overline{\Omega})}$ is uniformly bounded for $0 \leqslant \alpha \leqslant \Lambda$, so $\|f(\cdot, u+v)\|_{C^{1,\gamma}(\overline{\Omega})}$ is uniformly bounded. Rewrite (6.8) as

$$\mu \Delta w + \alpha \nabla f \cdot \nabla w + w(m-u-v) = 0 \quad \text{in } \Omega, \qquad \frac{\partial w}{\partial n} = 0 \quad \text{on } \partial\Omega. \tag{6.9}$$

By the Schauder theory [22] we see that $\|w\|_{C^{2,\gamma}(\overline{\Omega})}$ is uniformly bounded for $0 \leqslant \alpha \leqslant \Lambda$, from which it follows that $\|u\|_{C^{2,\gamma}(\overline{\Omega})}$ is uniformly bounded for $0 \leqslant \alpha \leqslant \Lambda$. $\square$

Remark 6.3. For precise statements of global Hölder estimates for conormal derivative problems, we refer to Lemma 5.1 of [37] for elliptic equations and Theorem 6.44 of [36] for parabolic equations. The proof of Lemma 5.1 of [37] can be found in Chapter 10 of [29, pp. 466–467].

Lemma 6.5. *Suppose that $\mu > \nu$. There exists some $\alpha_0 > 0$ small such that if $0 \leqslant \alpha < \alpha_0$, (1.4) has no positive steady states.*

Proof. We argue by contradiction. If not, suppose that there exist $\{(\alpha_k, u_k, v_k)\}_{k=1}^\infty$ with $\alpha_k \to 0+$ as $k \to \infty$, and $u_k > 0$ and $v_k > 0$ are equilibria of (1.4) with $\alpha = \alpha_k$. By Lemma 6.4, passing to a limit we may assume that $(u_k, v_k) \to (u_0, v_0)$ as $k \to \infty$, where $u_0 \geqslant 0$ and $v_0 \geqslant 0$, and

$$\mu \Delta u_0 + u_0(m - u_0 - v_0) = 0 \quad \text{in } \Omega,$$
$$\nu \Delta v_0 + v_0(m - u_0 - v_0) = 0 \quad \text{in } \Omega$$

with $\nabla u_0 \cdot n = \nabla v_0 \cdot n = 0$ on $\partial\Omega$. Since $\mu > \nu$, by [20] we cannot have both $u_0 > 0$ and $v_0 > 0$. Either we have $(u_0, v_0) = (\theta(\mu), 0)$, or $(u_0, v_0) = (0, \theta(\nu))$, or $(u_0, v_0) = (0,0)$. If $u_0 = v_0 = 0$, divide the equation of v_k by $\|v_k\|_{L^\infty}$ and pass to a limit (via a subsequence if necessary) to get $v_k/\|v_k\|_{L^\infty} \to v^* > 0$ in Ω as $k \to \infty$, where v^* satisfies

$$\nu \Delta v^* + m v^* = 0 \quad \text{in } \Omega, \qquad \nabla v^* \cdot n = 0 \quad \text{on } \partial\Omega. \tag{6.10}$$

Multiply (6.10) by $\theta(\nu)$ and integrate to get

$$\int\limits_{\Omega} v^* \theta^2(\nu) = 0$$

which is a contradiction. When $u_0 = \theta(\mu)$ and $v_0 = 0$, v^* satisfies

$$\nu \Delta v^* + \big[m - \theta(\mu)\big] v^* = 0 \quad \text{in } \Omega, \qquad \nabla v^* \cdot n = 0 \quad \text{on } \partial\Omega.$$

That is, the smallest eigenvalue of the operator $-\nu\Delta + (-m + \theta(\mu))$ with respect to zero Neumann boundary condition is equal to zero. So $1/\nu$ is the principal eigenvalue for

$$-\Delta\varphi = \lambda\big(m - \theta(\mu)\big)\varphi \quad \text{in } \Omega, \qquad \nabla \cdot n = 0 \quad \text{on } \partial\Omega.$$

However, the equation of $\theta(\mu)$ tells us that this eigenvalue is $1/\mu$, a contradiction.

If $u_0 = 0$ and $v_0 = \theta(\nu)$, divide the equation for u_k by $\|u_k\|_\infty$. Since a term of the form

$$\int\limits_{\Omega} \nabla\varphi \cdot \alpha_k \cdot \frac{u_k}{\|u_k\|_\infty} \nabla(m - u_k - v_k) \to 0$$

as $k \to \infty$ for any test function $\varphi \in C^1(\overline{\Omega})$ (since $\alpha_k \to 0$), we get $u^* > 0$ in Ω, $\nabla u^* \cdot n = 0$ on $\partial\Omega$ with

$$\mu \Delta u^* + u^*\big(m - \theta(\nu)\big) = 0$$

which is a contradiction (the argument is similar as the case $u_0 = \theta(\mu)$ and $v_0 = 0$). □

Proof of (2), Theorem 7. Hypothesis 2 of Theorem 12 is satisfied because we are working in a suitable Sobolev space; see [44]. To verify the Fredholm properties in hypotheses 1 and 3 we can follow the analysis in Example 4.2 of [44], which treats a cross-diffusion system with structure somewhat similar to our model. The key issue is to verify that the linear operators in those hypotheses satisfy suitable structure and ellipticity conditions. It turns out that those conditions involve only the principal parts of the operators and boundary conditions, that is, the terms in each operator or boundary condition involving the highest order derivatives. The principal part of the differential operator in $D_{(u,v)}F(\alpha, u, v)$ arising from linearizing (F_1, F_2), applied to (w_1, w_2), is

$$\begin{pmatrix} \mu + \alpha u & \alpha u \\ 0 & \nu \end{pmatrix} \begin{pmatrix} \triangle w_1 \\ \triangle w_2 \end{pmatrix}. \tag{6.11}$$

The boundary condition has principal part

$$\begin{pmatrix} \mu + \alpha u & \alpha u \\ 0 & \nu \end{pmatrix} \begin{pmatrix} \nabla w_1 \cdot n \\ \nabla w_2 \cdot n \end{pmatrix}. \tag{6.12}$$

These forms fit the structure shown in case 3 of Remark 2.5 of [44], where in the notation of [44],

$$a(x) = \begin{pmatrix} \mu + \alpha u & \alpha u \\ 0 & \nu \end{pmatrix} \tag{6.13}$$

and $\alpha_{ij} = \delta_{ij}$ where δ_{ij} is the Kronecker delta. It then follows by Theorem 2.7 and Corollary 2.10 of [44] that $D_x F(\lambda, x)$ is Fredholm provided that

$$det \begin{pmatrix} \mu + \alpha u + \sigma & \alpha u \\ 0 & \nu + \sigma \end{pmatrix} \neq 0 \tag{6.14}$$

for $(\alpha, u, v) \in V$ when $\sigma = 0$ or $arg\,\sigma \in [-\pi/2, \pi/2]$. The determinant is

$$(\mu + \alpha u + \sigma)(\nu + \sigma),$$

so since $\mu + \alpha u > 0$ on V, relation (6.14) is satisfied and hence $D_x F(\lambda, x)$ is Fredholm for all $(\lambda, x) \in V$, as needed for hypothesis 1.

The analysis for hypothesis 3 is similar. The principal part of $kD_x F(\lambda, x) + (1-k)D_x F(\lambda, x_0)$ evaluated at $x = (u_1, v_1)$ and $x_0 = (u_2, v_2)$, applied to (w_1, w_2), is

$$\begin{pmatrix} \mu + (1-k)\alpha u_1 + k\alpha u_2 & (1-k)\alpha u_1 + k\alpha u_2 \\ 0 & \nu \end{pmatrix} \begin{pmatrix} \triangle w_1 \\ \triangle w_2 \end{pmatrix}. \tag{6.15}$$

The principal part of the boundary condition is

$$\begin{pmatrix} \mu + (1-k)\alpha u_1 + k\alpha u_2 & (1-k)\alpha u_1 + k\alpha u_2 \\ 0 & \nu \end{pmatrix} \begin{pmatrix} \nabla w_1 \cdot n \\ \nabla w_2 \cdot n \end{pmatrix}. \tag{6.16}$$

By the definition of V we have $\alpha u_i > -\mu/2$ for $i = 1, 2$ so that $\mu + (1-k)\alpha u_1 + k\alpha u_2 > 0$. It follows as in (6.11)–(6.14) that $kD_x F(\lambda, x) + (1-k)D_x F(\lambda, x_0)$ is Fredholm of index 0 so that Theorem 12 applies to our system. It follows that the positive component $\mathcal{C}^+$ of the solution branch bifurcating at $\alpha = \alpha^*$ must satisfy one of the alternatives in the theorem. Alternative (ii) is impossible because of the uniqueness of α^*. We have not yet specified which complement of $N(D_x F(\lambda_0, x_0))$ we want Z to be. Recall that $N(D_x F(\lambda_0, x_0))$ is spanned by (φ^*, ψ^*) where $\varphi^* > 0$ in Ω. We may choose

$$Z = \left\{ (u, v) \in X \colon \int_\Omega u\varphi^*\,dx = 0 \right\}. \tag{6.17}$$

It follows from (6.17) that if $(u, v) \in Z$ then u must change sign. If alternative (iii) holds then since $x_0 = (0, \theta)$ it must be the case that there are solutions on $\mathcal{C}^+$ for which u changes sign. For points on $\mathcal{C}^+$ sufficiently close to $(\alpha^*, 0, \theta)$, we have $u > 0$. Thus, on $\mathcal{C}^+$, if (iii) holds then the minimum of u changes sign on $\mathcal{C}^+$. Since $X \subset C(\overline{\Omega})^2$, the function $G(u, v) = \min_{\overline{\Omega}} u$ is continuous on X, so since $\mathcal{C}^+$ is a connected component there must be a point (α, u_0, v_0) on $\mathcal{C}^+$ with $\min(u_0) = 0$. Let $w = e^{-(\alpha/\mu)(m-u_0-v_0)}u$. Then w satisfies

$$\mu\nabla \cdot \left[e^{(\alpha/\mu)(m-u_0-v_0)}\nabla w\right] + we^{(\alpha/\mu)(m-u_0-v_0)}(m - u_0 - v_0) = 0 \quad \text{in } \Omega, \qquad \nabla w \cdot n|_{\partial\Omega} = 0$$

with $\min_{\overline{\Omega}} w = 0$. By the strong maximum principle, $w \equiv 0$, so $u_0 \equiv 0$, which implies that alternative (ii) holds in Theorem 12. Alternative (ii) is ruled out by the uniqueness of the bifurcation point α^*. Thus, alternative (i) must hold. By Theorem 5 and Lemma 6.5, (1.4) has no positive steady states for $\alpha < \alpha_0$ and $\alpha > \Lambda_3$. In the definition of V, let $\delta < \frac{1}{2}\min\{\alpha_0, 1/\Lambda_3\}$. Then componentwise positive steady states of (1.4) along $\mathcal{C}^+$ cannot meet $\{\delta\} \times [W^{2,p}(\Omega)]^2$ and $\{1/\delta\} \times [W^{2,p}(\Omega)]^2$. If $(\alpha, u, v) \in \mathcal{C}^+ \cap V$ and $u > 0$ and $v > 0$, by Lemma 6.4, u and v are uniformly bounded in the $C^{2,\gamma}(\Omega)$ norm for some $\gamma \in (0, 1)$. Thus, to satisfy alternative (i), there must be some point $(\alpha, u, v) \in \mathcal{C}^+ \cap V$ such that either u changes sign or v changes sign. The case when u changes sign can be ruled out in the same way as before by applying the function $G(u, v) = \min_{\overline{\Omega}} u$. Therefore, the only possibility is that

v changes sign. Since $X \subset C(\overline{\Omega})^2$, the function $H(u,v) = \min_{\overline{\Omega}} v$ is continuous on X, so since $\mathcal{C}^+$ is a connected component, there exists some $(\alpha^{**}, u^{**}, v^{**})$ such that $\alpha^{**} \in (\delta, 1/\delta)$, $u^{**} > 0$ in Ω, $v^{**} \geqslant 0$ in Ω and $\min_{\overline{\Omega}} v^{**} = 0$. By the strong maximum principle, $v^{**} \equiv 0$ in $\overline{\Omega}$. This implies that u^{**} is a positive steady state of (1.1) with $\alpha = \alpha^{**}$. □

7. Asymptotic behaviors of bifurcation points

This section is devoted to the proofs of Theorems 8 and 9.

7.1. Proof of part (a), Theorem 8

We first establish the following result, which classifies the asymptotic behavior of $\lambda_u(\alpha, \mu, \nu)$ when $\alpha \to \infty$, $\alpha/\mu \to \infty$.

Proposition 6. *Suppose that $m > 0$ in $\overline{\Omega}$. Suppose that $\alpha \to \infty$, $\alpha/\mu \to \infty$.*

(i) *If we further assume that $\alpha/(\mu/\nu) \to 0$, then*

$$\lambda_u(\alpha, \mu, \nu) \cdot \frac{\alpha}{\mu} \to \frac{\int_\Omega m \ln m}{\int_\Omega m} - \max_{\overline{\Omega}} \ln m < 0.$$

(ii) *If we further assume that $\alpha/(\mu/\nu) \to \eta$ for some $\eta \in (0, \infty)$, then*

$$\lambda_u(\alpha, \mu, \nu) \cdot \frac{\alpha}{\mu} \to \lambda^*,$$

where λ^* is the smallest eigenvalue of

$$-\eta \Delta \varphi + \left[\frac{\int_\Omega m \ln m}{\int_\Omega m} - \ln m \right] \varphi = \lambda \varphi \quad \text{in } \Omega, \qquad \nabla \varphi \cdot n|_{\partial\Omega} = 0.$$

(iii) *If we further assume that $\alpha/(\mu/\nu) \to \infty$, then*

$$\lambda_u(\alpha, \mu, \nu) \cdot \frac{\alpha}{\mu} \to \frac{\int_\Omega m \ln m}{\int_\Omega m} - \frac{1}{|\Omega|} \int_\Omega \ln m > 0.$$

Proof. Set $\tilde{\lambda} = \lambda_u(\alpha, \mu, \nu) \cdot (\alpha/\mu)$. Then $\tilde{\lambda}$ is the smallest eigenvalue of the problem

$$-\frac{\alpha}{\mu/\nu} \Delta \psi + \frac{\alpha}{\mu} (\tilde{u} - m) \psi = \tilde{\lambda} \psi \quad \text{in } \Omega, \qquad \nabla \psi \cdot n|_{\partial\Omega} = 0.$$

We first establish part (i). Given any $\epsilon > 0$, by Lemma 3.1 we have that if α and α/μ are sufficiently large,

$$\frac{\int_\Omega m \ln m}{\int_\Omega m} - \ln m - \epsilon \leqslant \frac{\alpha}{\mu} (\tilde{u} - m) \leqslant \frac{\int_\Omega m \ln m}{\int_\Omega m} - \ln m + \epsilon$$

in $\overline{\Omega}$. Let λ_ϵ denote the smallest eigenvalue of the problem

$$-\frac{\alpha}{\mu/\nu} \Delta \psi + \left[\frac{\int_\Omega m \ln m}{\int_\Omega m} - \ln m + \epsilon \right] \psi = \lambda \psi \quad \text{in } \Omega, \qquad \nabla \psi \cdot n|_{\partial\Omega} = 0.$$

By the comparison principle of principal eigenvalues, $\tilde{\lambda} \leqslant \lambda_\epsilon$. It is well known that

$$\lim_{\frac{\alpha}{\mu/\nu}\to 0} \lambda_\epsilon = \min_{\overline{\Omega}}\left[\frac{\int_\Omega m\ln m}{\int_\Omega m} - \ln m + \epsilon\right].$$

Hence,

$$\limsup_{\frac{\alpha}{\mu/\nu}\to 0} \tilde{\lambda} \leqslant \min_{\overline{\Omega}}\left[\frac{\int_\Omega m\ln m}{\int_\Omega m} - \ln m + \epsilon\right].$$

Since ϵ is arbitrary, letting $\epsilon \to 0$ we have

$$\limsup_{\frac{\alpha}{\mu/\nu}\to 0} \tilde{\lambda} \leqslant \min_{\overline{\Omega}}\left[\frac{\int_\Omega m\ln m}{\int_\Omega m} - \ln m\right].$$

Similarly, we can show that

$$\liminf_{\frac{\alpha}{\mu/\nu}\to 0} \tilde{\lambda} \geqslant \min_{\overline{\Omega}}\left[\frac{\int_\Omega m\ln m}{\int_\Omega m} - \ln m\right].$$

This completes the proof of part (i).

For the proof of part (ii), since $\frac{\alpha}{\mu/\nu} \to \eta \in (0,\infty)$ and $(\alpha/\mu)(\tilde{u}-m)$ is uniformly bounded, we see that $\tilde{\lambda}$ is also bounded. We first normalize the positive eigenfunction ψ such that $\max_{\overline{\Omega}} \psi = 1$. By standard elliptic regularity and Sobolev's embedding theorem we may assume that, passing to a subsequence if necessary, $\psi \to \varphi$ in $C^2(\overline{\Omega})$ and $\tilde{\lambda} \to \hat{\lambda}$ as $\frac{\alpha}{\mu/\nu} \to \eta$ and $\alpha, \alpha/\mu \to \infty$, where φ and $\hat{\lambda}$ satisfy

$$-\eta\Delta\varphi + \left[\frac{\int_\Omega m\ln m}{\int_\Omega m} - \ln m\right]\varphi = \hat{\lambda}\varphi \quad \text{in } \Omega, \qquad \nabla\varphi\cdot n|_{\partial\Omega} = 0.$$

Since $\varphi \geqslant 0$ and $\max_{\overline{\Omega}} \varphi = 1$, we see that $\hat{\lambda}$ must be the smallest eigenvalue. Hence, $\hat{\lambda} = \lambda^*$. Since the convergence is independent of the choice of sequence, we see that part (ii) holds. The proof of part (iii) is similar to that of (ii), so we omit it. □

Lemma 7.1. *Fix $\nu > 0$. Then, $\alpha_u(\mu,\nu)/\mu$ is bounded as $\mu \to \infty$.*

Proof. We argue by contradiction. Suppose that $\alpha_u(\mu,\nu)/\mu \to \infty$ as $\mu \to \infty$. Hence, $\alpha_u \to \infty$. By part (iii) of Proposition 6, we see that

$$\lambda(\alpha_u,\mu,\nu)\cdot\frac{\alpha_u}{\mu} \to \frac{\int_\Omega m\ln m}{\int_\Omega m} - \frac{1}{|\Omega|}\int_\Omega \ln m > 0,$$

where the last inequality follows from Lemma 3.2. However, this is a contradiction as $\lambda(\alpha_u,\mu,\nu) = 0$. □

Proof of part (a) of Theorem 8. Set $w = e^{-(\alpha_u/\mu)(m-\tilde{u})}\tilde{u}$. Then w satisfies

$$\mu\nabla\cdot\left[e^{(\alpha_u/\mu)(m-\tilde{u})}\nabla w\right] + e^{(\alpha_u/\mu)(m-\tilde{u})}(m-\tilde{u})w = 0 \quad \text{in } \Omega, \qquad \nabla w\cdot n|_{\partial\Omega} = 0.$$

Since $\tilde{u}$ is uniformly bounded (see [9]), α_u/μ is bounded (Lemma 7.1) and $\mu \to \infty$, by standard elliptic regularity, we may assume that, passing to a subsequence if necessary, w converges to some positive constant, denoted by C (and thus $\tilde{u} \to u^*$ for some u^*), and $\alpha_u/\mu \to \tilde{\eta}$ such that

$$\begin{cases} e^{-\tilde{\eta}(m-u^*)}u^* = C \quad \text{in } \Omega, \\ \int_\Omega u^*(m-u^*) = 0, \\ \nu\Delta\varphi^* + (m-u^*)\varphi^* = 0 \quad \text{in } \Omega, \quad \varphi^* > 0 \quad \text{in } \Omega, \quad \nabla\varphi^* \cdot n|_{\partial\Omega} = 0. \end{cases} \tag{7.1}$$

If $\tilde{\eta} = 0$, then $u^* = \int_\Omega m/|\Omega|$. This implies that φ^* satisfies

$$\nu\Delta\varphi^* + \left(m - \int_\Omega m/|\Omega|\right)\varphi^* = 0 \quad \text{in } \Omega, \qquad \varphi^* > 0 \quad \text{in } \Omega, \qquad \nabla\varphi^* \cdot n|_{\partial\Omega} = 0. \tag{7.2}$$

Dividing (7.2) by φ^* and integrating in Ω, we have

$$\nu \int_\Omega \frac{|\nabla\varphi^*|^2}{(\varphi^*)^2} = 0,$$

which implies that φ^* is a constant. By (7.2) we see that $m = \int_\Omega m/|\Omega|$, which is a contradiction. Hence, $\tilde{\eta} > 0$.

Rewriting the first equation of (7.1) as

$$-\tilde{\eta}(m-u^*) + \ln u^* = \ln C$$

and substituting it into the second equation of (7.1), we find that

$$\ln C = \frac{\int_\Omega u^* \ln u^*}{\int_\Omega u^*}.$$

Therefore,

$$-\tilde{\eta}(m-u^*) + \ln u^* = \frac{\int_\Omega u^* \ln u^*}{\int_\Omega u^*}.$$

In particular, this implies that $\tilde{\eta} > 0$ and $u^* > 0$ satisfy

$$\begin{cases} \tilde{\eta}(m-u^*) = \ln u^* - \dfrac{\int_\Omega u^* \ln u^*}{\int_\Omega u^*}, \\ \nu\Delta\varphi^* + (m-u^*)\varphi^* = 0 \quad \text{in } \Omega, \quad \nabla\varphi^* \cdot n|_{\partial\Omega} = 0. \end{cases} \tag{7.3}$$

This completes the proof. $\square$

7.2. Proof of part (b), Theorem 8

It follows from Lemma 4.2 that $\alpha_v(\mu,\nu)/\mu \leqslant \eta^*$. Passing to some subsequence if necessary, we may assume that $\alpha_v(\mu,\nu)/\mu \to \overline{\eta}$ for some $\overline{\eta} \geqslant 0$ as $\mu \to \infty$. Note that by definition of $\alpha_v(\mu,\nu)$, the equation

$$\mu\nabla\cdot\left[e^{(\alpha_v/\mu)(m-\theta)}\nabla w\right] + e^{(\alpha_v/\mu)(m-\theta)}(m-\theta)w = 0 \quad \text{in } \Omega, \qquad \nabla w\cdot n|_{\partial\Omega} = 0$$

has a positive solution with $\max_{\overline{\Omega}} w = 1$. By standard elliptic regularity, we see that as $\mu \to \infty$, $w \to 1$ in L^∞. Integrating the equation of w in Ω, we find

$$\int_\Omega e^{(\alpha_v/\mu)(m-\tilde{v})}(m-\tilde{v})w = 0.$$

Passing to the limit in the above equation we have

$$\int_\Omega e^{\overline{\eta}(m-\theta)}(m-\theta) = 0;$$

i.e., $F(\overline{\eta}) = 0$. Hence, by Lemma 4.1 we see that $\overline{\eta} = \eta^*$, that is, $\alpha_v(\mu,\nu)/\mu \to \eta^*$ as $\mu \to \infty$. This completes the proof.

7.3. Proof of Theorem 9

We first show that $\alpha_u(\mu,\nu) \to \infty$ as $\nu \to 0$. If not, suppose that $\alpha_u(\mu,\nu)$ is bounded and we shall reach a contradiction. Set $w = e^{-(\alpha_u/\mu)(m-\tilde{u})}\tilde{u}$. Since $\tilde{u}$ is uniformly bounded in L^∞, we see that $\|w\|_{L^\infty(\Omega)}$ is also uniformly bounded. Note that w satisfies

$$\mu\nabla\cdot\left[e^{(\alpha_u/\mu)(m-\tilde{u})}\nabla w\right] + \tilde{u}(m-\tilde{u}) = 0 \quad \text{in } \Omega, \qquad \nabla w\cdot n|_{\partial\Omega} = 0.$$

By standard elliptic regularity, passing to a subsequence if necessary, we may assume that $w \to w^*$ and $\alpha_u \to \alpha^*$ such that w^* is a positive solution of

$$\mu\nabla\cdot\left[e^{(\alpha^*/\mu)(m-u^*)}\nabla w^*\right] + u^*\left(m-u^*\right) = 0 \quad \text{in } \Omega, \qquad \nabla w\cdot n|_{\partial\Omega} = 0,$$

where $w^* = e^{-(\alpha^*/\mu)(m-u^*)}u^*$. Since m is non-constant and $\int_\Omega u^*(m-u^*) = 0$, we see that $m-u^*$ must change sign in Ω. Recall the equation

$$\nu\Delta\psi + \psi(m-\tilde{u}) = -\lambda_u(\alpha,\mu,\nu)\psi \quad \text{in } \Omega, \qquad \nabla\psi\cdot n|_{\partial\Omega} = 0.$$

Similar to the proof of part (i) of Proposition 6, we can obtain

$$\lim_{\nu\to 0}\lambda_u(\alpha_u,\mu,\nu) = \min_{\overline{\Omega}}\left(m-u^*\right) < 0,$$

which contradicts $\lambda_u(\alpha_u,\mu,\nu) = 0$. Hence, $\alpha_u \to \infty$ as $\nu \to 0$.

Next, we rewrite the equation of ψ as

$$\frac{\alpha_u}{\mu/\nu}\Delta\psi + \frac{\alpha_u}{\mu}(m-\tilde{u})\psi = 0 \quad \text{in } \Omega, \qquad \nabla\psi\cdot n|_{\partial\Omega} = 0.$$

Table 1
Coexistence region: $\mu = 1$.

ν	Coexistence region for α
0.1	$[0.83, 0.89]$
0.01	$[5.1, 9.7]$
0.001	$[18.9, 98.6]$

Since $\alpha_u/\mu \to \infty$ and $\alpha_u \to \infty$, we can apply Proposition 6 to conclude that the only possibility is that $\alpha_u/(\mu/\nu) \to \tilde{\eta}$, where $\tilde{\eta}$ is some positive number such that the following equation has a positive solution:

$$-\tilde{\eta}\Delta\psi + \left[\frac{\int_\Omega m \ln m}{\int_\Omega m} - \ln m\right]\psi = 0 \quad \text{in } \Omega, \qquad \nabla\psi \cdot n|_{\partial\Omega} = 0.$$

By Lemma 3.2 we have

$$\int_\Omega \left[\frac{\int_\Omega m \ln m}{\int_\Omega m} - \ln m\right] > 0.$$

Since $\int_\Omega m \ln m / \int_\Omega m - \ln m$ is negative somewhere in Ω, the existence and uniqueness of such positive $\tilde{\eta}$ follows from standard theory for principal eigenvalue for indefinite weight functions [6].

8. Numerical simulations

In this section we assume that $\Omega = (0, 1)$ and numerically investigate the effect of fitness-dependent dispersal in four types of models: (i) system (1.4); (ii) a two-species competition model in which both species adopt random dispersal and fitness-dependent dispersal; (iii) a two-consumers–one-resource model in which both consumers move upward along the resource gradient but the resource species does not move; (iv) a tri-trophic predator–consumer–resource model in which both consumers move upward along the resource gradient but the predator and the resource do not move. Our simulation results suggest that for models (i), (ii) and (iii), selection favors stronger advection along the fitness gradient and slower random dispersal, while the opposite can occur for the model (iv). Our results may yield some insight into the evolution of dispersal in food chains, e.g., the presence of predation risk seems to have much larger impact on the evolution of dispersal strategies of consumer species than the presence of resource species.

8.1. Coexistence region in (1.4)

We consider the following two cases.

Case 1. Fix $\mu = 1$ and decrease $\nu = 0.1, 0.01, 0.001$. The corresponding coexistence intervals for α are summarized in Table 1. These results suggest that as $\nu \to 0$, the coexistence intervals become wider, and both ends of the coexistence interval tend to infinity as $\nu \to 0$. This is in agreement with Theorem 9.

Case 2. Fix $\nu = 0.1$ and increase $\mu = 1, 2, 5, 10, 20$. The corresponding coexistence intervals for α are summarized in Table 2. These results suggest that as $\mu \to \infty$, the coexistence intervals become wider, and both ends of the coexistence interval tend to infinity. These results agree with Theorem 8.

8.2. Fitness-dependent dispersal

We consider the scenario when both competing species adopt random dispersal and fitness-dependent dispersal as follows.

Table 2
Coexistence region: $\nu = 0.1$.

μ	Coexistence region for α
1	[0.83, 0.89]
2	[1.734, 1.889]
5	[4.47, 4.87]
10	[9.04, 9.85]
20	[18.2, 19.8]

$$\begin{cases} u_t = \big(\mu u_x - \alpha u(m-u-v)_x\big)_x + u(m-u-v) & \text{in } 0<x<1,\ t>0, \\ v_t = \big(\nu v_x - \beta v(m-u-v)_x\big)_x + v(m-u-v) & \text{in } 0<x<1,\ t>0, \\ \mu u_x - \alpha u(m-u-v)_x = \nu v_x - \beta v(m-u-v)_x = 0, & x=0,1,\ t>0, \end{cases} \tag{8.1}$$

where μ, ν, α, β are positive constants. Our numerical results suggest that the following holds: when $\alpha = \beta$, u survives and v dies if $\mu < \nu$, u dies and v survives if $\mu > \nu$; when $\mu = \nu$, u dies and v survives if $\alpha < \beta$, and u survives and v dies if $\alpha > \beta$. In other words, selection favors stronger advection along the fitness gradient and slower random dispersal.

8.3. Consumer and resource model

We performed numerical simulations on the following one-resource and two-consumer model

$$\begin{cases} R_t = R\big[r(x)\big(1 - R/K(x)\big) - a_1C_1 - a_2C_2\big] & \text{in } 0<x<1,\ t>0, \\ (C_1)_t = C_1(e_1a_1R - d_1) + \big[\mu_1(C_1)_x - \beta_1C_1R_x\big]_x & \text{in } 0<x<1,\ t>0, \\ (C_2)_t = C_2(e_2a_2R - d_2) + \big[\mu_2(C_2)_x - \beta_2C_2R_x\big]_x & \text{in } 0<x<1,\ t>0, \\ \mu_1(C_1)_x - \beta_1C_1R_x = \mu_2(C_2)_x - \beta_2C_2R_x = 0, & x=0,1,\ t>0, \end{cases} \tag{8.2}$$

where $R = R(x,t)$ and $C_i = C_i(x,t)$ $(i = 1,2)$ represent the density of a resource species and two consumer species, respectively. Our numerical results suggest some similar phenomena as those observed in model (8.1). Namely, assume that all parameters are the same except β_1 and β_2, then the competitor with the larger advection rate always drives the other competitor to extinction; if all parameters are the same except μ_1 and μ_2, then the competitor with the smaller random dispersal rate always drives the other competitor to extinction.

8.4. A tri-trophic model

We also considered a three trophic level food chain model of the form

$$\begin{cases} R_t = R\big[r(x)\big(1 - R/K(x)\big) - a_1C_1 - a_2C_2\big] & \text{in } 0<x<1,\ t>0, \\ (C_1)_t = C_1(e_1a_1R - d_1 - \alpha_1P) + \big[\mu_1(C_1)_x - \beta_1C_1R_x\big]_x & \text{in } 0<x<1,\ t>0, \\ (C_2)_t = C_2(e_2a_2R - d_2 - \alpha_2P) + \big[\mu_2(C_2)_x - \beta_2C_2R_x\big]_x & \text{in } 0<x<1,\ t>0, \\ P_t = P(f_1\alpha_1C_1 + f_2\alpha_2C_2 - d_p) & \text{in } 0<x<1,\ t>0, \\ \mu_1(C_1)_x - \beta_1C_1R_x = \mu_2(C_2)_x - \beta_2C_2R_x = 0, & x=0,1,\ t>0, \end{cases} \tag{8.3}$$

where the model consists of one resource species, two consumers and a top predator. The top predator feeds on two consumers and both consumers feed on the resource species. The two consumers move, but the top predator and the resource species do not. Our numerical results for (8.3) suggest something different from the previous models. Namely, assume that all parameters are the same except β_1 and β_2, then the competitor with the smaller advection rate drives the other competitor to extinction; if all parameters are the same except μ_1 and μ_2, then the competitor with the larger random dispersal rate can drive the other competitor to extinction.

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